Population Dynamics and Trophic Ecology of Two Species of Australian Desert Rodents

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A thesis submitted for the degree of Doctor of Philosophy at the University of Sydney, Sydney, N.S.W., Australia.

The University of Sydney

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La gloria di colui che tutto move
per l'universo penetra, e risplende
in una parte più e meno altrove.
Nel ciel che più de la sua luce prende
fu' io, e vidi cose che ridire
né sa né può chi di là sù discende……

Dante Alighieri, *La Divina Commedia*, Paradiso,
Canto I, XIV century

Abstract

This study used field data and laboratory experiments to investigate the role of food and trophic behaviour in controlling the population dynamics of two native Australian rodent species, *Pseudomys hermannsburgensis* and *Notomys alexis*, in the Simpson Desert, south-western Queensland. Some of the data and specimens used in this study were collected over a period of twelve years by Dr C. R. Dickman (*pers. comm.*). The other data were collected during laboratory experiments and analyses by myself from 1998 to 2002.

Pattern analyses were used on a twelve-year dataset from the Simpson Desert to investigate the relationship between rainfall and population dynamics of the two study species.

Modified cumulative monthly rainfall residuals were correlated with capture rates of the rodents across twelve sites, and the rodent response to rain was shown to be spatially and temporally variable. At some sites rodents responded with delays of 3-6 months to rainfall events, as documented previously in other studies; however, rodents did not inevitably increase in abundance after heavy rainfall events.

Three models were proposed to explain the variable response of rodents to rainfall, and examined in turn. The first model proposed that rainfall increases availability of free water and consequently rodent numbers. This model was refuted based on empirical observations that rodents show no consistent response to the presence of free water. The second model suggested that rainfall increases vegetation cover, and thus allows rodents to escape predation, exploit a greater range of microhabitats, and gain access to improved burrowing conditions. Rainfall and rodent capture rates were predicted to be correlated with plant cover, but rodent diets were expected not to change with changes in plant cover. Analyses showed that plant cover was correlated with rainfall and rodent capture rates, but also that rodent diets changed with plant cover in a non-linear way. These findings provided partial support for the second model. The third model was a classical bottom-up model, and predicted that rainfall would increase food availability and accessibility to rodents, and consequently rodent numbers. Analyses showed that Food resources were correlated with rainfall but not clearly with capture rates of the two rodent species. These findings provided partial support for the third model.

The foraging strategies of the two species were investigated during periods of high, decreasing, low and increasing densities with special emphasis given to describing the granivorous portion of their diets. The two species had different dietary strategies at

different phases of their cycles and seemed to partition their food resources by using different microhabitats.

To investigate the ability of the study rodents to detect water in food, selection experiments were performed to test the ability of captive rodents to detect moist seeds. Both species selected seeds with the highest water content. These results further invalidate the first model predicting that rodents are water-limited.

Six separate seed selection experiments were conducted on the same individual rodents, using a total of 30 native seed species collected in the desert. The thirteen most preferred species over the trials were then offered all together in a final experiment, to observe how the seed selection changed with the number of species presented. Water content, energy, ash, and nitrogen content, linear dimensions, weight, proportion of the edible part of the seed (embryo) of the entire seed (embryo plus husk), and handling time, were measured for each seed species. These data were then compared with the rank of each species in the selection, to identify any patterns of choice for particular seed characteristics. Changes in selection pattern were observed with changes in the number of species offered. Both rodent species selected native seed species based on their water content, protein, largest linear dimension (LLD), and largest kernel/entire seed ratio. Moreover, they were not constrained by seed handling time.

The ability of rodents to detect buried seeds was tested in experiments where seeds were provided at different depths and with clumped and scattered dispersions. The two dispersions were exploited in different ways at different depths by the two species. On the surface, both species consumed more scattered than clumped seeds, but exploited clumped seeds more than scattered seeds at depths of 2-3 cm.

The results of pattern analyses suggested that spinifex seed was abundant during population eruptions of the two study rodents, and that it formed part of the diet of both species. In order to test the influence of spinifex seed on the reproductive success of the desert rodents, and consequently its role in triggering rodent eruptions, two different diets were tested on *Pseudomys hermannsburgensis*. Six captive-bred pairs were fed a diet based on spinifex and mixed seeds. Another six captive-bred pairs were fed a standard diet of mixed seeds. The mating time, the size of litter, the weight of young, and the weaning time were recorded and compared between the two treatments. No significant differences were observed between the two diets with respect to most reproductive parameters, probably because of low statistical power due to small sample sizes. However, the spinifex-enhanced diet, which was higher in protein, tended to have a stimulating effect on the

breeding pairs in that they produced larger litters in a shorter time, and also litters that were male-biased. Further investigations are warranted on the stimulatory effects of food constituents on reproductive output.

In conclusion, I suggest that the two study species are likely to be limited by nutrients and that food quality rather than quantity plays a major role in driving their population dynamics. The lack of a linear correspondence between changes in primary productivity and changes in rodent numbers may be due to the quality of food resources that are available after rain; food quantity may not reflect the amount of food that is apparently available. I also suggest that other factors may interact to render the scenario more complex than the simplistic bottom-up models proposed. Elucidation of these factors, and their interactions, will provide exciting challenges for future researchers.

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Title Photograph: Buffo, *Notomys alexis*

Photographer: Pavel German

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CHAPTER 1: GENERAL INTRODUCTION

1.1. Introduction

This thesis describes the population dynamics of two species of rodents in the Simpson Desert of central Australia. It evaluates the role of environmental factors, primarily rainfall and food, in driving population fluctuations, and also describes how the study species track and exploit food resources. In the sections below I first describe desert environments and adaptations of desert biota in general, and then focus on the key questions to be addressed in the present work.

1.1.1. What is a desert?

The word "desert" evokes images of an arid and inhospitable land, characterised by sparse vegetation and scarcity of water. Often high temperatures and sandy substrates are associated with this image. In reality, desert ecosystems are far more complex. Water (mainly in the form of precipitation) is the main component that shapes desert features, while its lack (aridity) can be used to define arid environments with some precision. For instance, Koppen deserts are areas where annual rainfall is less than 254 mm, and with high air temperatures (Leopold 1961). Emberger (1942) defined a true or extreme desert as having a highly irregular seasonal rhythm of rainfall, with droughts lasting longer than 1 year. Evenari (1981) stressed further that all deserts have unpredictable rainfall with irregularities being extreme in terms of quantity, temporal and spatial pattern. Shmida (1985) classified extreme deserts as areas that receive an annual rainfall of less than 70 mm, true deserts as areas receiving between 70 and 120 mm, and semi-deserts as areas receiving between 120 and 400 mm. Other authors also define "desert" in terms of aridity, but consider that other characteristics such as solar radiation, geology, soils, and topography are important in the classification (e.g. Whitford 2002).

Thornthwaite (1948) developed a moisture index or index of aridity based on the difference between precipitation and the evapotranspiration potential of natural vegetation. Meigs (1953) later used Thornthwaite's index to categorise the arid and semi-arid areas of the world, but included in his index the season of rainfall, maximum air temperature in the hottest month and minimum temperature in the coldest month. Three levels of aridity are

described by this index: extremely arid, arid and semi-arid. This system has received widespread acceptance, with the world's deserts usually located in Meigs' arid and extremely arid areas (Dick-Peddie 1991). Furthermore, Meigs' index roughly coincides with a more recent and refined index devised by Shmida (1985), thus achieving some consistency in how desert environments are characterised.

1.1.2. Deserts of the world

Desert ecosystems occupy one-quarter to one-third of the world's land surface (Crawford 1981), and are located within two great belts that almost encircle the earth on either side of the equator. Hydrologically, the belts are open high-pressure systems that develop under the influence of worldwide air circulation patterns; thus, they have no well-defined boundaries. In summer, the systems move toward the equator; consequently, particularly in North America, they are invaded by humid tropical air, which produces high-intensity storms of brief duration. In winter, the pressure systems drift poleward and are often invaded by frontal storms of characteristic low intensity and long duration (Thames and Evans 1981). The northern system is located between 10 and 50 degrees latitude, and the southern system between 20 and 30 degrees latitude (Thames and Evans 1981). Consequently, the majority of the world's deserts are located around the Tropic of Cancer and Tropic of Capricorn, 15° - 35° north and south of the equator. Hot deserts are usually located between latitudes 20° and 35° and cold deserts between 65° and 90° (Degen 1997). There are 14 temperate to hot desert systems in the world, if the massive and heterogeneous area that stretches from northern Africa to China is considered as one arid to semi-arid continuum. These systems vary greatly in size, climate, substrate, and biota (Table 1.1).

1.1.3. Australian deserts

The Australian desert environment is classified as subtropical, and is maintained by stable high pressure cells (Hadley cells) lying between 30° N and 30° S (Smith 1984). Australian deserts extend over much of the central part of the continent, reaching the coast in the northwest, and covering a total area of about 3.4 million km^2. Desert accounts for about 44% of the country and semi-arid areas for another 37% (Williams 1979a, b).

Table 1.1. Physical characteristics of world deserts

Desert	Latitudinal range (°)	Area (Km²)	Annual rainfall (mm)	Temperature range (°C)	Geology, soil types, topography and vegetation	References
Africa						
Sahara	22-32 N	9.1 million	<25.4 mm	Max: up to +58°C	Regs – plains of gravels and pebbles Hammadas – flat areas covered by flag-stones Ergs – extensive sand seas Chenopod – *Zygophyllum* desert Dwarf shrubs; *Artemisia* and Poaceae on sands	Le Houérou 1979, 1986 Mitchell 1984 Cloudsley-Thompson 1984 Evenari 1985 Heatwole 1995 Degen 1997
Kalahari-Karoo	21-28 S	450,000	150-500 mm	Winter range: -14 - +30°C Summer range: +5 - +45°C	Dunefields support shrub savannah Areas unusually rich in trees Succulents in some parts	McGinnies *et al.* 1970 Lovegrove 1993 Heatwole 1995 Degen 1997
Namib	18-30 S	13,000	5-185 mm	<0 - >+40°C	Wide seas of mobile sand Rocky hills and mountains Narrow, sandy littoral strip Pebbly to sand flats Succulent desert dwarf shrubs	Lovegrove 1993 Heatwole 1995 Degen 1997

Desert	Latitudinal range (°)	Area (Km²)	Annual rainfall (mm)	Temperature range (°C)	Geology, soil types, topography and vegetation	References
Asia						
Arabian	15-31 N	2.6 million	35-100 mm	Average in summer: 45°C Average in spring and autumn: 29°C	Stony mountains Deep valleys Two great sand seas Chenopod – *Zygophyllum* desert Dwarf shrubs; *Artemisia* and Poaceae on sands	Mandaville 1986 Heatwole 1995 Degen 1997
Iranian	27-36 N	390,000	50-200 mm	Annual average 15-18°C Max summer: 45-50°C	Coarse, undeveloped, often deep, sometime saline, with low organic content Rocky areas, gravel pavements and sands Chenopod-*Artemisia* steppes and pygmy open woodland	Zohary 1973 Kaul and Thalen 1979 Heatwole 1995 Degen 1997
Thar	24-31 N	600,000	100-500 mm	Winter range: +4-+10°C Summer range: +24->+40°C	Sand plains, finely textured soils, low barren hills, sand dunes, rocky flat terrains Thorny-rattanoid savannah	Gupta 1986 Heatwole 1995 Degen 1997
Turkestan	36-47 N	1.9 million	70-160 mm	-7 - +17°C	Alluvial and loess plains and depressions Two great sandy areas and two smaller sandy areas Fine-textured soils, some saline, black and red sands *Artemisia-Stipa* steppes and pygmy open woodland	Heatwole 1995 Degen 1997

Desert	Latitudinal range (°)	Area (Km²)	Annual rainfall (mm)	Temperature range (°C)	Geology, soil types, topography and vegetation	References
Asia (continued)						
Takla-Makan	36-43 N	337,600	<10-400 mm	-30 - +30°C	Moving dunes Chenopod desert dwarf shrubs	Walter and Box 1983 Li *et al.* 1989 Zhou *et al.* 1989 Degen 1997
Gobi	42-47 N	957,400	50-250 mm	-45 to +36°C Annual average: -2- -6°C	Gravelly and pebbly plains and sand dunes Stony slopes Coarse-textured, non-saline soils, with accumulations of lime Chenopod-Tamarix desert shrubland	Weiner and Gorecki 1981 Heatwole 1995 Degen 1997
Australia	21-33 S	3.4 million	127-265 mm	<-7 - >+40°C	Hummock grassland, trees, tall shrubs	Heatwole 1995 Degen 1997
North America						
Great Basin	35-42 N	190,000	240 mm	-8 - +35°C Annual average +9.8°C	Spaced bushes, sometimes grasses and forbs Often a single species of shrub dominates the desert communities	Heatwole 1995 Degen 1997

Desert	Latitudinal range (°)	Area (Km²)	Annual rainfall (mm)	Temperature range (°C)	Geology, soil types, topography and vegetation	References
North America (continued)						
Mojave	35-36 N	54,000	56-165 mm	Summer range: <+23 - >+38°C Winter range: <0 - >+21°C	Cactus and leaf succulents	Norris 1976 Heatwole 1995
Sonoran	25-33 N	120,000	120-300 mm	Biseasonal rainfall pattern Max in summer: >+40°C	Microphyllous shrubs, trees, cacti and/or leaf succulents (agaves and yuccas) Sandy dunes with grassy and shrubby vegetation	Crosswhite and Crosswhite 1982 MacMahon and Wagner 1985 Heatwole 1995 Degen 1997
Chihuahuan	23-32 N	175,000	200-300 mm	+13 - +20°C	Microphyllous shrubs, fleshy rosetted shrubs (mainly agaves), cacti and grasses Sclerophyllous brushwood and low coniferous woodland	Medellín-Leal 1982 Heatwole 1995 Degen 1997
South America						
Atacama	7 N-35 S	360,000	<12.7 mm	-2 - +26°C	Rocky desert without vegetation in the northern coastal region Cactus "forest" at higher elevations. Infertile coastal dunes	Heatwole 1995 Degen 1997

Desert	Latitudinal range (°)	Area (Km^2)	Annual rainfall (mm)	Temperature range (°C)	Geology, soil types, topography and vegetation	References
South America (continued)						
Monte	23-30 S	380,000	188-330 mm	+7 - +22.4°C Annual average: +13.7°C	Mountains, flat valleys, and closed basins Muddy depressions, saltpans, dunes, slopes, badlands, alluvial cones and tablelands Thorny succulent savannah	Bailey *et al.* 1977 Heatwole 1995 Degen 1997
Patagonia	37-47 S	150,000	<200 mm	Annual average: +5 - +9°C	Gravelly tablelands divided by valleys Low cushion-like shrubs in the desert Spaced clumps of grasses in the steppe	Heatwole 1995 Degen 1997

According to Meigs' index of aridity (Meigs 1953) Australian deserts are arid, but not extremely arid. Rainfall is moderate and highly variable both spatially and temporally. Periods of exceptional rainfall are infrequent but often are followed by periods of extended drought (Morton 1982, Stafford Smith and Morton 1990). The northern half of the arid zone receives summer rainfall and the southern half winter rainfall. Winters are mild and summers hot (Evenari 1985, Shmida 1985, Williams and Calaby 1985). Australian desert soils are poor in nutrients in comparison to other arid regions of the world (Winkworth 1967, Charley and Cowling 1968, Stafford Smith and Morton 1990). Nutrients are concentrated in the top 5-10 cm of the soil and in areas of rainfall run-on (Stafford Smith and Morton 1990).

The Australian arid zone can be divided into six major deserts: the Simpson, Sturt, Great Victoria, Gibson, Great Sandy and the Tanami (Williams and Calaby 1985). The Simpson Desert in the centre, the Great Sandy Desert in the northwest, and the Great Victoria Desert in the southwest are sandy deserts. They have characteristically long, parallel sand dunes lying on sandy plains, sometimes with surface gravel or stones. The two major stony deserts are the Gibson Desert, lying between the Great Sandy and the Great Victoria deserts, and Sturt's Stony Desert southeast of the Simpson.

The vegetation of arid Australia is often dominated by more trees and tall shrubs than in other deserts. The most arid areas of Australia comprise hummock grassland. This vegetation type consists largely of perennial, evergreen, sclerophyllous grasses of the genus *Triodia* (spinifex), which have a unique form: they grow in large hemispherical clumps, or hummocks, with spiny-tipped leaves pointing outward. The ground between hummocks is often bare (Heatwole 1995). As moisture increases from central Australia outward, there is a gradient to low *Acacia* shrubland, chenopod shrubland and tussock grassland, progressively to scrub or tall shrubland (Heatwole 1995).

1.1.4. Life in deserts

Productivity depends on rainfall, with sporadic or limited productivity characterising desert communities (Louw and Seely 1982). Seely (1978) reported a linear correlation between production and rainfall, with an increase in production of 0.75 to 49.92 g m^{-2} occurring for an increase of 18 to 98 mm in rainfall. An important concept is also the minimum annual precipitation necessary to assure that any production will occur. Several studies have tried to quantify this threshold (Noy-Meir 1973, Seely 1978, Webb *et al.*

1978), with the observed range being between 10.6-75 mm yr^{-1} (Louw and Seely 1982). Secondary production is also controlled by the amount of water available in the environment. For many animals, intake of free water is necessary if the food they consume is too dry (Beatley 1976, Hamilton *et al.* 1977, Low 1979). Water has a limiting effect even on growth and reproduction. Rain is almost always the main trigger of germination in perennials and annuals (Louw and Seely 1982). In addition, some birds, insects, snails and other animals interpret rain as a signal to begin reproduction (Immelmann 1963, Yom-Tov 1971). While precipitation can be used roughly to predict net primary and secondary production, other factors also influence productivity. The quality of available food, in particular the protein content, can be another limiting factor (Seely and Louw 1980, White 1993, 2002). Thus, net primary production may not always simply mean food, because plant species may be nutritious for only a short period of time (Sinclair 1975).

Nutrients represent another critical factor in desert ecosystems. Noy-Meir (1974) examined the reasons for nutrient scarcity and consequently their vital importance: most of the available nutrients may be engaged in the rapid pulse of growth of perennials and especially annuals, and thus are exhausted quickly; some desert soils are naturally low in nutrients, especially in nitrogen and phosphorous (Charley and Cowling 1968, Wallace *et al.* 1978, West and Skujins 1978, Stafford Smith and Morton 1990, White 1993); nutrients are concentrated mainly at the surface because of low rates of decomposition and leaching, and consequently are less available to plant roots and more easily removed by water and wind erosion (Stafford Smith and Morton 1990); nutrients are often very localised, because vegetation cover, and hence litter decomposition, is very sparse and patchy, and because of wind action. Radiation, temperature and wind may also affect and limit production. The actions of these abiotic factors can be intense and prolonged, and consequently may often limit the optimal growth of plants and animals (Noy-Meir 1973, Louw and Seely 1982).

Because of climatic unpredictability and usually low primary productivity, deserts are often seen as relatively simple ecosystems marked by low species diversity and the absence of strong biological controls and feedback (Noy-Meir 1974, 1980, Seely and Louw 1980, Wallwork 1982, Whitford 1986); desert communities also are viewed as being primarily controlled by abiotic factors (Noy-Meir 1973, 1974, 1980, 1985, Brown *et al.* 1979b). However, while insufficiency of water limits traditional agriculture (Thames and Evans 1981), desert animals and plants have adapted to these environments, and under particular conditions can be extraordinarily diverse. The surprising diversity of some taxa,

strong spatial and temporal heterogeneity in species abundances, and a varied array of biotic interactions suggest that deserts are often relatively complex and biologically rich places (Polis 1991, Brown and Ernest 2002). The adaptive responses to desert conditions among plants and animals from the various continents are often evolutionarily convergent. Both related and unrelated animal and plant species have developed, through parallel evolutionary processes, comparable forms and structures that permit survival in similar ecological niches (Thames and Evans 1981). Despite these convergences, however, associations within plant and animal communities can still distinguish each desert (Mares 2002).

1.1.4.1. Desert plants

Plants that survive in deserts have to face restricted water availability, low relative humidity, nutrient paucity, and huge temperature fluctuations during the 24 hour cycle. Such plants are likely to have evolved from mesophytic ancestors and to have developed both physiological and morphological adaptations to xeric environments (Harris and Campbell 1981). Several classifications of desert plants have been proposed, based on their strategies for survival. One such classification distinguishes lichens, herbaceous perennials, shrubs, trees, annuals, and succulents. Major features of these groups are summarised in Table 1.2.

1.1.4.2. Desert animals

Desert heterotrophic organisms are limited by the same constraints experienced by plants. They are also unable to produce their own food, thus being dependent on the primary productivity generated by autotrophs at the base of the food web. As noted above, plant productivity, and consequently the presence and distribution of heterotrophic organisms, is strongly linked to the availability of water, and often limited by it. Water is not cycled within the local system, but passes through it, coming in as rain, fog or dew and leaving convectively by evaporation or transpiration. Thus, it represents a periodically exhaustible resource replenished only by new input. If the inputs are irregular, they produce a fluctuating availability of resources with episodic periods of plenty followed by unpredictable, long intervals of deprivation. Animals respond to such systems with a vast range of morphological, physiological and behavioural adaptations:

Table 1.2. Major adaptations of desert plants

Growth form	Roots	Leaves	Flowers	Adaptations	Plant qualities	References
Lichens Flat, on bare rocks or soil surfaces	Rootless	Crusty surfaces	Absent	Absorption via the thalus of rain, dew, air moisture, nitrogen dissolved in rain, minerals in direct contact, and dust.	Pioneer plant Important in soil formation	Harris and Campbell 1981
Perennials (herbaceous perennials, shrubs, trees) Erect	Long, extended roots. Rhizosheaths (persistent root hairs and sheaths of sand grains that cover the root, promoting water absorption and nitrogen fixation due to microbial activity)	Thick, waxy cuticle, sunken and few stomata, leaf area reduced at a minimum, lack of deciduous leaves	Only small proportion of florets produces seeds	Substrate instability adaptations: vegetative mobility, production of vertical leafy rhizomes, adventitious roots, rapid germination and elongation of parts of the plant are all adaptations to substrate Water scarcity adaptations: thick epidermis, thick cuticle and waxes, corky bark, sclerenchyma, secondary structures (scales, hairs, mucilage) to insulate from evaporation and protect from solar radiation and abrasion, dormancy, dew, fog, and condensed water absorption Saline and alkaline soil adaptations: lowered osmotic potential of cell contents, discarding of salt in water of guttation or via special glands and cells, concentration of salt under the crowns, excretion onto leaf surface and discard through leaf fall or rainstorms washing.	Rich in carbon-based inhibitory compounds (tannins, lignins, sclerophyll), poor in nutrients, poorly digestible	Beadle 1966 Goodin and Mozafar 1972 Jacobs 1973 Lyshede 1977, 1979, Halle *et al.* 1978 Wullstein *et al.* 1979 Harris and Campbell 1981 Westoby 1980 Fahn 1982 Louw and Seely 1982 Beard 1984 New 1984 Coley *et al.* 1985 Southwood *et al.* 1986 Tilman 1986 Westoby 1988 Stafford-Smith and Morton 1990 Fahn and Cutler 1992 Danin 1996 Shephard 1999

Growth form	Roots	Leaves	Flowers	Adaptations	Plant qualities	References (continued)
Annuals (grasses and forbs) Erect	Shallow, fibrous, without storage organs or heavily suberised exterior cellular structures	Succulent, broad, simple in shape, large number of stomates, thin cover of epidermal cells	Present	Rapid germination and growth to mature flowering plants after rainfall. Prompt exploitation of available resources during wet periods Production of vast amount of seeds in short period of time Germination of seeds is inhibited by biochemical controls (immaturity, high temperature, high light intensity) to avoid the risk of germination after poor rains	Rich in nutrients, very low structural carbon present in the tissues.	Harris and Campbell 1981 Shephard 1999
Succulents Erect or prostrate	Shallow, near the soil surface	Thick cuticle covers the plant body	Present	Stomates open at night to reduce water loss. Absorption and storage of water from small amounts of precipitation Root hairs dry up during drought to avoid water movement from plant to dry soil. Very slow growth	Flowers and seeds are produced without much new growth. High free water content in the tissues.	Harris and Campbell 1981

1. Movement from areas in drought to those having received a pulse of rain (escape, migration, nomadism)
2. Adoption of a "pulse-reserve" system where they opportunistically alternate between an active state during periods of high input and an inactive and resistant state (diapause, dormancy, torpor) during low production
3. Exploitation of certain temporal niches to avoid hot temperatures by day (retreat, reduced diurnality, nocturnality, crepuscularity, bimodal activity)
4. Use of burrows, shelters, refugia with a more buffered microclimate and humidity than the exterior environment
5. Living in social colonies (ants, termites)
6. Use of specialised adaptations (colour, locomotor strategies, body orientation, sun-basking, fog-basking, heat and cold tolerance, heterothermy, adjustments to their osmoregulation, metabolism, respiration and transpiration)
7. Adoption of flexible, opportunistic feeding habits, using whatever resource happens to be available at any particular time (omnivory).

Animals may use one or several of the listed strategies to cope with the desert environment. Examples are shown in Table 1.3.

1.1.5. Foraging in deserts

As noted above and in Table 1.3, flexible or opportunistic feeding habits should often increase the fitness of individual foragers in desert environments. Where food resources are scant and patchy, as in deserts, opportunism should be a successful foraging strategy to exploit favourable conditions whenever they occur (MacArthur 1972, Louw and Seely 1982, Shmida *et al.* 1986). In arid environments, therefore, opportunistic trophic strategies are very common. I examine desert trophism more closely in this section.

One prediction of optimal foraging theory is that "animals should forage in ways that maximise net energy intake per unit of feeding time under both good and poor conditions" (Heatwole 1995). Several subsidiary predictions follow from this. Thus, animals will select the more energetically valuable foods among those available, and will include less preferred items in their diet only if more highly preferred foods are not available. Animals will usually choose larger food items, but may shift to smaller items during food shortage. Animals also will be more selective when satiated or resources are abundant, exploiting a greater variety of taxa of food items with increasing food scarcity. Selectivity will increase

Table 1.3. Major adaptations of desert animals

Strategy	Species examples	Main features	References
Movement:			Pennycuick 1975
emigration	Birds, large mammals (e.g. wildebeest, springbok), locusts	Seasonal migrations following rain	Hamilton *et al.* 1977
			Cloudsley-Thompson 1978
nomadism	oryx		Louw and Seely 1982
			Costa 1995
"Pulse-reserve" system	Crustacea	Diapause	Leopold 1962
	Heteromyids (*Microdipodops* and *Perognathus*)	Dormancy (aestivation in hot, arid environments, and/or hibernation in cold environments) and torpor (reduced oxygen uptake)	Schmidt-Nielsen 1964
			Ruibal *et al.* 1969
	Marsupials: *Cercartetus concinnus* and some Dasyuridae	Dormancy and torpor	Louw and Seely 1982
	Birds (*Phalaenoptilus nuttallii*)	Dormancy	Harris *et al. 1984*
	Reptiles	Aestivation, reduction of metabolic rate	French 1993
	Amphibans	Dormancy to remarkable depths (>1.5 m) beneath the surface, reduction of metabolic rate	Degen 1997
Temporal niches			
Retreat (bimodal activity rhythm)	Tenebrionid beetles	Diurnality for thermophilous species, nocturnality for hygrophilous species	Hamilton 1975
			Langford 1983
	Heteromyids (*Dipodomys*), rodents	Foraging the first hour after sunset and then several hours before dawn	Scholtz and Caveney 1988
			Reichman and Price 1993
Nocturnality	Heteromyids (*Dipodomys* and *Perognathus*), other rodents	Active only an hour nightly	Costa 1995
			Degen 1997
Diurnality	Invertebrates, reptiles, rodents, lagomorphs, hyraxes	Active only during the day	

Strategy	Species examples	Main features	References
Temporal niches (continued)			
Crepuscularity		Active during transitional periods between day and night	
Seasonal modulation of the activity rhythm		Shift between a bimodal activity rhythm in summer to a unimodal rhythm in winter	
Refuges	Rodents	Burrows near the base of bushes or on sand plains, variability in the structural complexity of the burrow (no chamber, chambers without nests, nests with chambers, system of branched tunnels)	Norris 1958 Lawrence 1959 Nagy 1959 Pope 1960 Ghobrial and Hodieb 1973 Eisenberg 1975 Naumov and Lobachev 1975 Wallwork 1982 Kucheruk 1983 Happold 1984 Bennett *et al. 1988* Conti *et al.* 1995 Costa 1995
	Gerbils and heteromyids	Burrows as food storage areas	
	African rodent mole (*Cryptomys damrensis*), Jerboa (*Jaculus jaculus*), *Pygeretmus pumilio*	Nests at different depths, and consequently at different temperatures during different seasons	
	Invertebrates, amphibians, reptiles, and birds	Construction of nests or holes or utilisation of burrows of other animals	
	Psammophilous animals (tenebrionid beetles, sand roaches, lizards, snakes, marsupial and golden moles)	Penetration into the sand, without building burrows	
	Skinks, lacertids, iguanids, agamids, and sand dwelling grasshoppers	Burial in the sand	
Eusociality	Ants, Termites	Nest as storage areas to buffer food paucity of low productivity periods Construction of mounds around the nest to improve thermoregulation Communal defence tactics against predation Alternation between vigilance and repose	Ettershank 1971 Grigg 1973 Wilson 1990 Costa 1995
	Rodents	Social behaviour such as huddling together to improve thermal conditions	

Strategy	Species examples	Main features	References
Eusociality (continued)	Dromedary camels	Crouching in groups to reduce the total body surface exposed to solar radiation	
Specialised adaptations			Bartholomew 1956
Morphological	Jack rabbit, Saharan fennec, North American kit fox, Australian rabbit bandicoot, desert rodents	Increase in size of extremities and appendages to ease heat dissipation (Allen's rule)	Khalil and Abdel-Messeih 1959 Chew 1961 Hudson 1962
	Small mammals	Decrease in body mass with an increase in aridity to maximise the heat dissipation surface (Bergmann's rule), long, thick pelage for improved insulation of their relatively higher surface area	Kirmiz 1962 Hemingway 1963 Schmidt-Nielsen 1966
	Arthropods, reptiles, birds, mammals	Morphological barriers (cuticle, scales, feathers and pelage) to minimise heat and water loss and heat gain through the body surface	Porter 1967 Calder and Schmidt-Nielsen 1967 MacMillen and Lee 1967
	Amphibians	Use of skin cocoons during aestivation, secretion of lipid film on to the skin surface, presence of a dense layer of chromatophores to reduce water loss	Mayhew 1968 Louw *et al. 1969*
	Diurnal Tenebrionid beetles	Use of melanin in the cuticle (black coloration) confers both waterproofing and strengthening properties	Taylor 1969 Shkolnik and Borut 1969
	Insects, Namib desert lizard	Long legs to increase the space between the ventral surface and the ground	Cloudsley-Thompson 1970 Loveridge 1970
	Tenebrionid beetles, Heteromyidae, Pedetidae, Dipodidae, Muridae	Rapid running, bipedalism	Taylor 1970 MacMillen and Lee 1970
Behavioural	Springbok (*Antidorcas marsupialis*)	When foraging body orientated towards the sun to reduce the profile area exposed to direct solar radiation	Ahearn 1970
	African ground squirrel (*Xerus inauris*)	When foraging use of the tail to shade the body	

Strategy	Species examples	Main features	References
Behavioural (continued)	Tortoises, quokka	Use of saliva for evaporative cooling	McGinnis and Voigt 1971
	Reptiles, invertebrates, birds (North American roadrunner)	Sun-basking to gain and store heat after cold nights	Riedesel *et al.* 1971
	Invertebrates, Namib beetles (*Onymacris unguicularis, Lepidochora discoidalis)* Namib jackals, Namib sand-diving lizard *Aporosaura anchietae*, Australian *Moloch horridus*	Fog-basking to collect condensed water droplets Direct collection of fog-water from sand, plants, rocks, air	Louw and Holm 1972 Taylor 1972 Collins and Bradshaw 1973 Bell *et al.* 1974 Cloudsley-Thompson 1974
Physiological	Anurans	Water absorption via hygroscopic skin	Sturbaum and Riedesel 1974
	Arthropods, reptiles	Isoenzymes (spectrum of enzymes, with similar functions, but with different thermal tolerance)	Hamilton 1975 Henwood 1975
	Large mammals	Shivering thermogenesis to survive cold periods. Muscular contractions produce metabolic heat	Penrith 1975 MacMillen and Christopher 1975
	Small mammals, heteromyids (*Dipodomys ordii*)	Non-shivering thermogenesis produces metabolic heat by freezing chemical energy, using mainly fats	Shkolnik *et al.* 1975 Hamilton and Seely 1976
	Large mammals: camel, eland, oryx, Sinai goats, Grant's gazelle	Heterothermy allows fluctuations in body temperature, thus being less dependent upon evaporating cooling	Seely and Hammilton 1976 Riddle *et al.* 1976 Cade and Maclean 1976
	Small mammals: *Spermophilus leucurus, Citellus leucurus, Acomys cahirinus, Dipus aegiptus, Notomys alexis, Rattus villosissimus, Gerbillus pusillus, Ammospermophilus leucurus*	Increase in temperatures tolerated better because of the wider thermal neutral zone (range of air temperatures at which the metabolic rate of an animal is minimal)	Shoemaker and Nagy 1977 McClanahan *et al.* 1978

Strategy	Species examples	Main features	References
Physiological (continued)	Reptiles, large herbivorous mammals (camel, dromedary, Indian zebu cattle, blackhead Persian sheep, North African and Middle Eastern sheep), Dasyurids	Fat storage to produce energy, metabolic water and insulation. In large mammals subcutaneous fat can retard heat loss by radiation and convection and in reptiles it can retard the flow of heat from the surface to the viscera, thus it is stored in special parts of the body and cavities (abdominal cavity, tail, humps, rump)	Marsh *et al.* 1978 Choshniak and Shkolnik 1978 Coutshié and Crowe 1979 Heinrich 1979 Heinrich and Bartholomew 1979 Riddle 1979 Robinson 1980 Finch *et al.* 1980 Henderson and Loveridge 1980 Shkolnik *et al.* 1980 Withers *et al.* 1980 Chappell and Bartholomew 1981 a, b Hewitt 1981 Louw and Seely 1982 Alicanta *et al.* 1982 Berman 1985 Buffenstein and Jarvis 1985 Buffenstein *et al.* 1985 Gettinger *et al.* 1986 Seely 1987
	Frogs, tortoises, sand-diving Namib lizard	Hypo-osmotic urine in the bladders	
	Reptiles	Water storage in tissues, including the blood	
	Ruminant mammals: black Bedouin goat	Water storage in the rumen	
	Amphibians Reptiles: *Varanus griseus,* tortoise *Gopherus agassizii*	High tolerance to dehydration (losses up to 40-50% of body water)	
	Small desert mammals	High tolerance to dehydration (losses up to 20-30% of body mass)	
	Camel, *Camelus dromedaries,* Bedouin goat	High tolerance to dehydration (losses up to 30% of its total body water), because they lose relatively small amounts of water from the plasma and are thus able to maintain a normal blood circulation during dehydration Recovery from desiccation also very rapid, the animal being capable of drinking enormous amounts of water and of restoring its original mass in minutes	
	Arthropods	Extremely dry faecal matter and uric acid (excreted in an almost dry crystalline state)	
	Spiders and scorpions	Guanine	

Strategy	Species examples	Main features	References
Physiological (continued)	Amphibians and mammals	Excretion of urea (ureotelic)	Cloudsley-Thompson 1991 Cloudsley-Thompson 1993 Louw 1993 French 1993 Steudel *et al.* 1994 Costa 1995 Hainsworth 1995 Degen 1997
	Insects, reptiles and birds	Excretion of uric acid (uricotelic)	
	Small desert rodents, *Notomys alexis*	Production of very high urine concentration (24 times its plasma concentration). Modification of the kidney (the loop of Henlé, thicker medulla)	
	Birds, desert lizards	Nasal salt gland which can excrete a solution of high osmolarity	
	Arthropods	Spiracles as respiratory adaptations	
	Mammals	Turbinals (a series of thin, convoluted sheets of bones) in the nasal cavity to minimise water loss during respiration	
	Camel, ostrich	Expiration of unsaturated breath	

with distance from nests, burrows or storage areas, because animals should seek energy-rich or larger prey in order to compensate for the energy expended in travelling (Kotler and Brown 1988, Heatwole 1995). According to these predictions, animals can either exploit high-energy or large food items, or minimise the time and/or energy expended in finding, manipulating, consuming, harvesting and transporting food (Heatwole 1995). For species that are less adapted to endure heat or desiccation stresses, or that are more susceptible to predation, time minimisation should be more important than energy maximisation (see review by Polis and Yamashita 1991). The risks of dehydration and predation can cause reduction of the time of exposure or lead to the exploitation of specific temporal niches. Nocturnality of many desert animals is a clear example of this. Classifying dietary categories is often very difficult because only a few animal species consume a single type of food (Degen 1997). Season, physiological condition and habitat can also affect the dietary strategies of animals, mainly as a result of differences in food availability.

Herbivory is the foraging strategy of animals that feed on vegetation. However, because the types of vegetable matter are various, this category is very heterogenous, including other more specific subcategories such as folivory (leaf-eater strategy), nectarivory (nectar or pollen-eater strategy), frugivory (fruit-eater strategy), granivory (seed-eater strategy), and detritivory (detritus-eater strategy) (Costa 1995, Degen 1997). Many desert insects are herbivorous in the general sense, feeding on plant matter (Costa 1995, Degen 1997). Strict herbivory (grasses and forbs-eater strategy) is typical of a large number of medium-sized and large mammals (e.g. ungulates); small mammals often can not digest enough herbage to satisfy their energy demands, especially in dry areas where forage is often of poor nutritive value (Degen 1997). Medium-sized herbivorous mammals are relatively numerous in the Australian and North American deserts (Morton 1979), with 18 species in Australia, mainly marsupials (Macropodidae), and 19 species in North America, some of which are ruminants (Ruminantia). Only four rodent species (murids) are herbivorous in Australia, but those in North America are more numerous, and include Geomyidae, and a number of Cricetidae (*Neotoma* spp., and *Sigmodon* spp.) (Morton 1979). Dipodidae (bipedal rodents of Asian deserts), Cavidae (rodents of South American deserts), Arvicolidae (voles common in several deserts), and Cricetidae are also herbivores (Degen 1997). Other fossorial rodents feed on subterranean parts of plants, and are present in many world deserts (Degen 1997). Other vertebrate herbivorous taxa of arid areas include reptiles, birds, primates and bats (Costa 1995).

Granivory is the strategy adopted by seed-eaters, that is species with diets composed of more than 50% seeds. Insects, birds and mammals are the main granivorous taxa (Costa 1995), sometimes competing among each other (Brown *et al.* 1979a, Morton and Baynes 1985). Among mammals, granivory appears to be an exclusive foraging strategy of rodents, in particular the smaller species (Degen 1997). In the North American, North African and Negev deserts mammals are the main granivorous taxa (Mares and Rosenzweig 1978, Abramsky 1983, Mares 1993), removing, at least in North America, more than 75% of the seed bank (Chew and Chew 1970, Soholt 1973, Nelson and Chew 1977, Brown *et al.* 1979b). In South America, Australia, and southern Africa, instead, ants are the main granivores (Mares and Rosenzweig 1978, Morton 1985, Kerley 1991, Kerley and Whitford 1994), with small mammals consuming as little as 0.5% of seed production (Kerley 1992).

Insectivory and carnivory (insect-eater strategy, and meat-eater strategy) are strategies that provide highly digestible diets with a high yield of metabolisable energy per unit intake (Degen 1997). In addition, fresh meat and animal tissues are very rich in water, enabling the animal that ingests them to be independent of free water (Bartholomew and Dawson 1968). These considerations suggest that these two strategies are ideal for desert life, and in particular for small desert animals. Many desert invertebrates are carnivorous (Costa 1995, Heatwole 1995). Adult amphibians are primarily generalist insectivores, including many Australian desert frogs (Calaby 1960), and some South African species (Fitzsimons 1935), as are many reptiles (Costa 1995). Insectivory is the most widespread strategy among birds, followed by granivory, and then finally strict carnivory (birds of prey) (Costa 1995). Among small mammals only a few marsupials are primarily carnivorous, such as the Patagonian opossum *Lestodelphis halli*, the grey four-eyed opossum *Philander frenata*, the grey short-tailed opossum *Monodelphis domestica*, and the Australian dasyurids (Schmidt-Nielsen 1964, Morton and Baynes 1985, Jones and Barmuta 1998, Hume 1999, 2003, Astúa de Moraes *et al.* 2003, Jones *et al.* 2003). Desert Insectivora and microchiropteran bats also prey principally on insects (Fisher 1941, Prakash 1959, Ross 1961, Hoffmeister and Goodpaster 1962, Costa 1995).

Omnivory is perhaps the most advantageous strategy in highly unpredictable environments. Animals do not select for single categories of food, but take prey from various categories depending on their availability. Proportions of items in the diet should shift seasonally subject to nutritional requirements (Karasov 1985). Various Carnivora, such as coyotes, jackals, foxes, and mustelids are generalist omnivores (Costa 1995).

Many medium-sized and small mammals are also omnivorous, such as the above-mentioned taxa of Carnivora, primates (Kummer 1968), and small desert rodents (Bar *et al.* 1984, Murray and Dickman 1994a, Costa 1995). In a comparison of small mammals of North American and Australian deserts, Morton (1979) and Morton *et al.* (1994) pointed out that North American communities were dominated by granivores, while Australian communities were richer in omnivorous and insectivorous species. They explained this by suggesting that climatic peculiarities of the Australian arid zone, and its high variability in seed production, may make granivory a difficult way of life for Australian murids that are consequently forced to consume a much more varied diet than the North American heteromyids (Morton and Baynes 1985). Availability of resources, rather than evolutionary specialisation, may be more significant in determining dietary patterns for rodents in arid environments (Murray and Dickman 1994a, Murray *et al.* 1999). Murray and Dickman (1994a) analysed the diet of two Australian rodent species, *Pseudomys hermannsburgensis* and *Notomys alexis*, and found that, while seeds were a major component of the diet of both species, in autumn the two species consumed a greater proportion of invertebrates (close to 50% of the total amount for *Notomys alexis* and 55-60% for *Pseudomys hermannsburgensis*). Consequently they concluded that the two species were omnivorous. Opportunism has also been observed in dasyurid marsupials in arid Australia (Fisher and Dickman 1993). High climatic unpredictability can favour dietary opportunism (i.e. omnivory) in many animals (Murray and Dickman 1994a, Murray *et al.* 1999).

1.1.6. Population dynamics and fluctuations in deserts

In many environments, animal populations, especially small mammals, exhibit large fluctuations in size over relatively short periods of time (e.g. Elton 1942, Shelford 1943, Pearson 1971, Hörnfeldt 1978, Keith and Windberg 1978, Southern 1979, Hansson and Henttonen 1985, Boutin *et al.* 1986, Henttonen *et al.* 1989, Krebs *et al.* 1992, Stenseth and Ims 1993, Hörnfeldt 1994, Fryxell *et al.* 1998, Dickman *et al.* 1999). Such fluctuations may be extreme in arid environments, and have been described especially among rodent species in South America (e.g. Péfaur *et al.* 1979, Fuentes and Campusano 1985, Meserve *et al.* 1995, Jaksic *et al.* 1997) and Australia (Newsome and Corbett 1975, Masters 1993, Dickman *et al.* 1999). The causes of such dramatic changes in abundance have been at the centre of much debate (e.g. Kareiva 1989, Pimm 1991, Krebs 1996, Hastings 1997). Both

intrinsic (Christian 1950, Chitty 1960, Boonstra 1994) and extrinsic (Andrewartha and Birch 1954, Lack 1954, Dickman *et al.* 1999) factors are thought to be involved. However, as sympatric species of small mammals and birds often show synchronous fluctuations (Elton 1942, Hörnfeldt 1978, Lindén 1988, Brown and Zeng 1989, Sheftel 1989, Jiménez *et al.* 1992, Hörnfeldt 1994), these taxa are likely to be driven by common and extrinsic factors that control changes in abundance of their populations. Weather, interactions with other animals (predation, competition, parasitism) and refuge availability are among the many factors that can influence population growth (Andrewartha and Birch 1954), and may often act synergistically (Errington 1946, Desy and Batzli 1989, Krebs *et al.* 1995a). For many populations, however, food represents the most immediate factor influencing population growth, by changing rates of reproduction or mortality (Lack 1954, White 1978, 1993). Numerous experiments investigating the effect of food addition on small mammal species (see Boutin 1990) have demonstrated that populations increase due to increases in reproduction (Newsome 1970, Desy and Batzli 1989), survival (Flowerdew 1972, Krebs *et al.* 1986, Dickman 1989) or both (Cole and Batzli 1978, Ford and Pitelka 1984). As discussed previously, rainfall is a critical determinant of primary and secondary production, especially in deserts. Eruptions of herbivorous and granivorous rodents often follow periods of exceptional rainfall and subsequent increases in food availability (Chew and Butterworth 1964, Beatley 1969, Newsome and Corbett 1975, Péfaur *et al.* 1979, Fuentes and Campusano 1985, Jiménez *et al.* 1992, Meserve *et al.* 1995, Jaksic *et al.* 1997, Dickman *et al.* 1999). However, small mammals may also show no response to rainfall (Meserve and Boulenge 1987, Dickman *et al.* 1999). The relationship between density of insectivorous species and rainfall is more complex and responses are not always guaranteed (Finlayson 1933, White 1978, Miles *et al.* 1982, Jiménez *et al.* 1992, Masters 1993, Reid *et al.* 1993, White 1993, Dickman *et al.* 2001).

Many species of Australian desert rodents exhibit large, non-cyclic, population fluctuations (Finlayson 1941, Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999). Plomley (1972) distinguished between plagues of *Rattus villosissimus* that move into the arid zone, and the natural in situ increase in numbers of other native desert rodents. The former species is not a "real" desert-dweller, because it depends on free water (Baverstock 1976). Instead, the latter species, as permanent residents of the arid zone, show some of the typical adaptations to desert habitats, and show periodic, large population fluctuations. The most common species undergoing such fluctuations include *Pseudomys australis* (Finlayson

1941, Brandle and Moseby 1999, Brandle *et al.* 1999), *Pseudomys hermannsburgensis* (Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999, Murray *et al.* 1999), *Notomys mitchellii* (Sturt 1849, Watts 1972, Cockburn 1981, Watts and Aslin 1981, Carthew and Keynes 2000, Seebeck and Menkhorst 2000), *Notomys cervinus* (Spencer and Gillen 1912, Watts 1970, 1972, Morton *et al.* 1994, Kelt *et al.* 1996, Cole and Woinarski 2000), and *Notomys alexis* (Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999, Murray *et al.* 1999). Several studies have proposed that the increase of primary productivity after rainfall is a likely cause of population increases (Finlayson 1941, Plomley 1972, Newsome and Corbett 1975, Masters 1993, Predavec and Dickman 1994, Brown and Ernest 2002). This thesis will deal with possible links among rainfall, food availability and rodent population dynamics.

1.1.7. Rodents of the Australian deserts

Due to the very high temporal variability of rainfall from year to year, scarcity of soil nutrients, and correlated high variation in food availability, arid Australia is an extreme environment where desert-dwellers are subject to strong but sporadic food limitation (Predavec 1994a, b). Australian desert rodents are likely to be particularly exposed to fluctuations in food because they do not show obvious adaptations to overcome long periods of food shortage, unlike other Australian desert taxa (Collins 1983, Morton 1985, Stafford Smith and Morton 1990) or desert rodents from other continents (de Graaf 1981, Downs and Perrin 1989, Randall 1993, Reichman and Price 1993). They do not use torpor to face long droughts (MacMillen and Lee 1970, MacMillen *et al.* 1972, Lee *et al.* 1981 but cf. Predavec 1997b). With few exceptions (e.g. *Zygomys* species) they do not store much food within the body (Watts and Aslin 1981, M. Predavec *pers. comm.*) or, by caching, in the environment (e.g. Price *et al.* 2000). In order to understand the foraging strategies used by Australian desert rodents and the factors that drive their population dynamics, it is important to investigate both their foraging ecology and responses to food with respect to other influential variables of the desert ecosystem (rainfall, nutrients, vegetation) (Stafford Smith and Morton 1990).

1.2. Thesis aims and structure

While the cause of dramatic fluctuations of rodent populations in arid Australia is still to be understood, rain-induced pulses of food resources are likely to be one of the main drivers of population outbreaks. The focus of my thesis is on the trophic ecology of two species, the spinifex hopping mouse *Notomys alexis* and sandy inland mouse *Pseudomys hermannsburgensis*, and more specifically on the role that rain-induced increases in desert plant seeds may play in modifying their population dynamics. Moreover, because spinifex (*Triodia basedowii*) represents the most abundant grass species for certain periods of the year, especially after rainfall, contributing a large part generally to the diet of desert rodent species, I try to clarify the importance of this plant species in the diet and in triggering the population eruptions of *Notomys alexis* and *Pseudomys hermannsburgensis*. My study aims specifically to:

- describe rodent population dynamics in relation to the abundance of grass seeds in the environment and in the diet,
- investigate foraging behaviour and dietary preferences for grass and other seeds based on water content and other seed characteristics, and
- determine experimentally the role of grass seed in triggering reproduction in *Pseudomys hermannsburgensis*.

It is of particular interest to identify the temporal changes in desert rodent populations that make them vulnerable to predation, human pressure and disturbance, and other external factors. It is also important to identify particular adaptations and foraging behaviour in an extreme desert environment, in order to gain insight into how best to conserve and manage native desert species.

The thesis is divided into nine chapters. Chapter 2 presents the description of the study sites and the study species. Chapter 3 describes patterns of population dynamics of the two species at different sites in the study area, the Simpson Desert of central Australia, correlating them with rainfall. In chapter 4, gut contents are compared with seed availability to understand the foraging strategy of the two species during peaks, troughs, increases and decreases of their populations. Experiments in chapter 5 test the ability of the two species to detect differences in moisture and to choose seeds with higher water content. Chapter 6 examines experimentally the possible factors that underlie seed selection by the two species, and the importance that nutrients and morphological characteristics may have in diet choice by rodents. Experiments in chapter 7 investigate the

ability of the two species to find seeds buried at different depths in the sand. They also examine how such ability changes with seed dispersion. Chapter 8 presents the breeding experiment on *Pseudomys hermannsburgensis*. This tries to clarify the importance of spinifex seed in triggering reproduction in this species of desert rodent, and so in driving population eruptions. Finally, chapter 9 reviews the results and conclusions of the entire thesis, providing interpretations and suggestions on whether and how essential plant material and seeds are in driving rodent population dynamics.

CHAPTER 2: STUDY AREA AND STUDY SPECIES

2.1. Study Area

The Simpson Desert is a sand desert in the north-eastern region of the arid zone. It covers approximately $1.7x10^5$ square kilometres, and it is centred on the state boundaries of Queensland, South Australia and the Northern Territory. Most of the desert is characterised by dune-fields (Shephard 1992). Sand dunes are oriented parallel in a NNW/SSE direction, as a result of prevailing winds primarily from the south-east (Twidale and Wopfner 1990). Dunes run for tens to hundreds of kilometres and are 200-1000 m apart and 10-40 m high (Purdie 1984). A single large study area of over 4000 km² was established. This area comprised 12 local sampling stations, or sites, 10-25 km apart, centred on Ethabuka Station, 130 km WNW of Bedourie, but extending also onto neighbouring Carlo, Tobermorey and Cravens Peak Stations. All fieldwork was carried out on these properties. The area is representative of much of arid Australia (Williams and Calaby 1985), and thus was considered suitable to study the association between rodent population dynamics and rainfall.

Sites names and locations were Ethabuka (23°45'30"S 138°28'30"E), Carlo (23°29'S 138°32'20"E), Cravens Peak (23°16'15"S 138°17'E), Field River North (23°45'07"S 138°00'54"E), Field River South (23°50'04"S 138°04'26"E), Koonamuka Swamp East (23°20'49"S 138°15'18"E), Koonamuka Swamp West (23°20'34"S 138°13'53"E), Naibar (23°39'08"S 138°17'37"E), Plum Pudding (23°13'16"S 138°27'56"E), South Site (23°50'41"S 138°23'59"E), Tobermorey East (23°25'31"S 138°00'01"E), and Tobermorey West (23°30'27"S 137°52'39"E) (Figure 2.1). Sites each contained 2-12 sampling grids covering 1 ha. From time to time during this study, habitat varied even markedly in floristic composition and vegetation abundance depending on the amount of rain received and the fire history, creating a patchy environment and clear differences between sites.

Vegetation in the Simpson Desert is diverse. Shephard (1992) recorded 789 plant species from 75 families. The dominant vegetation in the Simpson Desert is hummock grassland (Beard 1984, Bridgewater 1987, Lange and Fatchen 1990), often referred to as spinifex grassland, although the genus *Spinifex* itself is not present in these areas (Williams 1979a). At all twelve sites the dominant species is *Triodia basedowii*, hard spinifex (Crocker 1946,

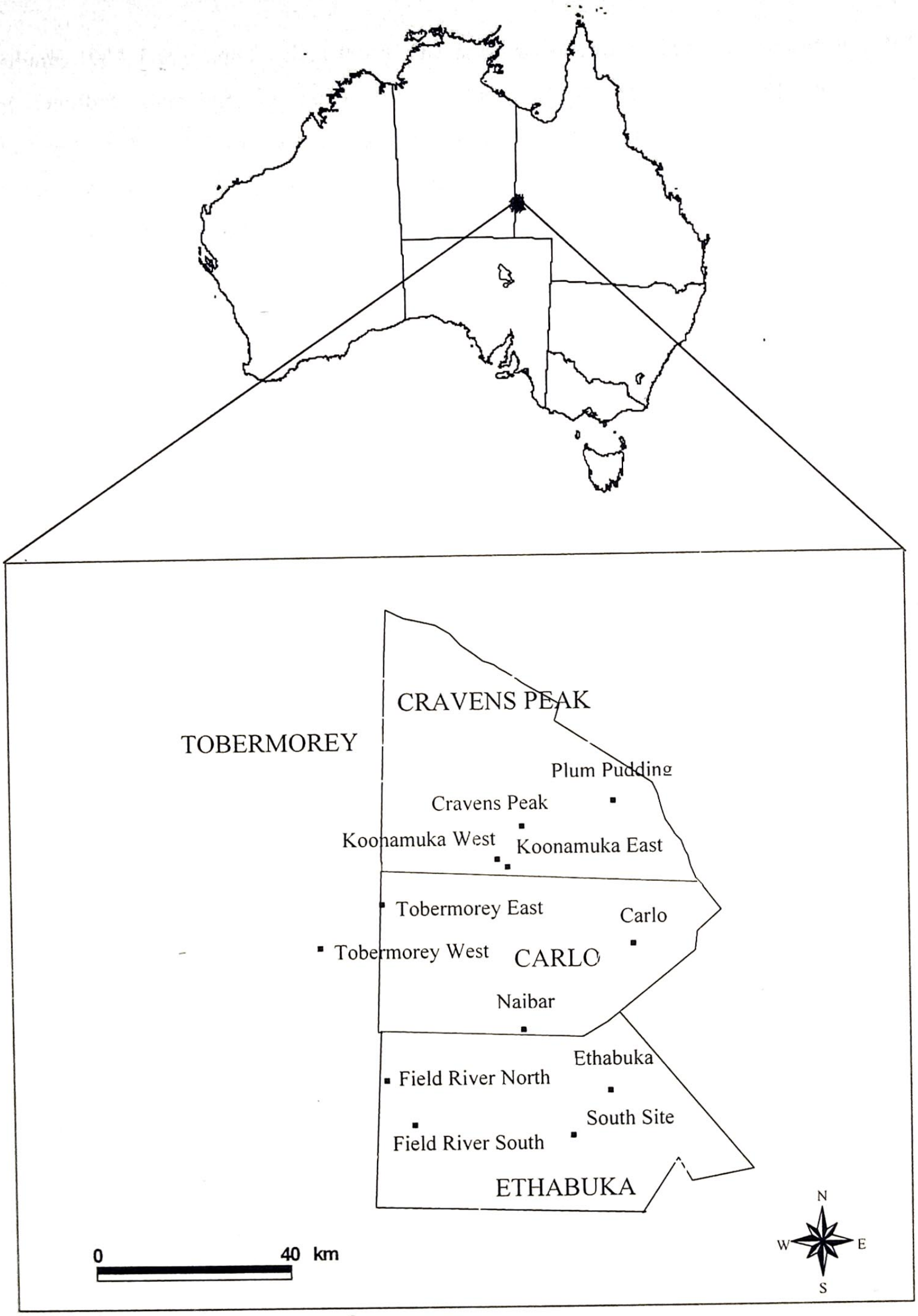


Figure 2.1. The twelve study sites on Ethabuka, Carlo, Tobermorey and Cravens Peak Stations, in the Simpson Desert, western Queensland.

Williams 1982, Lange and Fatchen 1990). This species can create a ground cover of over 30% and contribute over 96% of the biomass of the standing crop (Winkworth 1967). It is prominent in the swales between dunes, but sparser on the dune sides. Other species are *Acacia georginae* (gidgee), common in the clay soils between dunes, *Crotalaria* spp., *Grevillea stenobotrya* and *Zygochloa paradoxa* (canegrass), that occur on the upper dune sides. The dune crests are relatively bare because of their instability due to drifting sands, although after heavy rainfall ephemerals such as *Trachymene glaucifolia* and *Euphorbia* spp. can cover the dune sides and tops. Other grasses such as *Aristida* spp. and *Eriachne aristidea* increase on the dune sides and swales after abundant rainfalls, and may cover the surface of the normally bare gidgee flats (Purdie 1984, Shephard 1992).

Climatic data were obtained from the nearest long-term weather stations at Marion Downs (23°21'54"S, 139°39'06"E), and Glenormiston (22°55'S, 138°49'E). Temperatures shift from 38°C in December and January (summer average daily maximum), with a maximum of 50°C recorded on-site, to 7°C in July (winter average daily minimum). Rainfall is highly unpredictable with infrequent periods of high rainfall and subsequent periods of drought. Rain occurs mainly in summer, with more than 74% falling between October and March. The annual averages are 201 mm at Marion Downs and 218 mm at Glenormiston.

The Simpson Desert fauna comprises seven species of rodents, nine species of marsupials (eight dasyurids and one macropod) (Dickman *et al*. 1993), over thirty-eight species of lizards (Downey and Dickman 1993), ten species of snakes, and six species of frogs (Predavec and Dickman 1993). A high diversity of birds is also likely (Reid *et al*. 1990; Shephard 1992), but a complete survey of the area is lacking. High densities of feral cats and foxes have been observed, following explosions of desert rodent and marsupial populations (Dickman 1996a, Dickman *et al*. 1999). Cattle, dingos and camels are also present in the dune-fields.

2.2. Study Species

Of the seven rodent species recorded in the Simpson Desert, the two most common are *Pseudomys hermannsburgensis* and *Notomys alexis*. These two species are the subjects of this study.

Pseudomys hermannsburgensis (Waite), the sandy inland mouse, belongs to the tribe

Conilurini (subfamily Hydromyinae) that invaded the continent from Indonesia at least seven million years ago (Godthelp 1989). This quadrupedal species is one of the smallest members of the genus *Pseudomys*, and resembles the introduced House Mouse, *Mus domesticus* (Strahan 1998). Its adult body weight ranges 9-13 g, with a mean of 12 g (Breed 1983a). Its distribution covers much of arid central, eastern and western Australia. It is often found in hummock grassland (Masters 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999), but occurs in other habitats, including mulga flats, alluvial flats, Mitchell grass, acacia woodlands and mallee shrubland (Finlayson 1941, Watts and Aslin 1974, Denny 1975, Burbidge *et al.* 1976, Watts and Aslin 1981, Gibson 1986, Gibson and Cole 1988). However, the species prefers sandy and friable soils, where it forages close to, or under, vegetation cover (Dickman 1993). M. Predavec (unpublished data) found that animals are particularly active in the swales or on the sides of dunes, avoiding dune tops. The species forages by night, but with reduced activity under moonlight (M. Predavec unpublished data). A minimum of five to a maximum of twenty-two individuals have been found to share common burrows (Finlayson 1941, Watts and Aslin 1981), suggesting that the species is social and that tolerance amongst individuals changes with reproductive condition (Watts and Aslin 1981). In captivity females show low acceptance towards males after breeding, and may cannibalise their own litters (S. Ricci, unpublished data). In order to escape extreme temperatures and live in a moist environment, *P. hermannsburgensis* digs burrows up to 0.5 m deep, associated with bases of shrubs and small trees (Dickman 1993). In addition, it is likely that the species shifts the burrow depth over the year, moving to shallower burrows in winter (C.R. Dickman *pers. comm.*). *Pseudomys hermannsburgensis* survives desert conditions using a range of behavioural and physiological adaptations that reduce water loss and energy expenditure (MacMillen *et al.* 1972, McNab 1979). The species does not drink free water, but is able to extract moisture and metabolic water from its food. Urine is extremely concentrated (MacMillen *et al.* 1972). The lifespan of *P. hermannsburgensis* in captivity is about four years.

The species is an aseasonal breeder, showing opportunistic reproductive activity at all times of year (Finlayson 1941, Philpott and Smyth 1967, Taylor and Horner 1970, Breed 1990b). The species breeds from three months of age (Watts and Aslin 1981). In captivity, the oestrous cycle varies from 7-13 days and gestation is 29-34 days. Females have four teats, but

litter size can be as high as six, although the usual number is three or four (Watts 1979a, 1982). The weaning time is approximately 30 days. The species is principally omnivorous (Murray *et al.* 1999), but with the major portion of the diet made up of seeds. Plant material and invertebrates can represent more than 50% of the species' diet during certain periods of the year. Seasonal changes in diet reflect the opportunistic strategy of this species (Murray and Dickman 1994a).

Low recapture rates of this species (6.8%) suggest that individuals are highly mobile and that populations are not stable over long periods (Dickman *et al.* 1995). Long-range movements occur at all times of the year, but during or after rainfall the species has been found to move ~20% further than during dry periods. Many studies in arid Australia have documented strong fluctuations of desert rodent numbers, with increases occurring usually after rainfall (Finlayson 1939, Plomley 1972, Carstairs 1974, 1976, Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994a, b, Predavec and Dickman 1994, Dickman *et al.* 1999). Large eruptions of *P. hermannsburgensis* were recorded in the Simpson Desert in the winters of 1991 and 1992, with a six month lag after rainfall (Predavec 1994b, Dickman *et al.* 1999). The species increased with a similar pattern at two other sites in arid Australia, with variation in response time following rainfall (Dickman *et al.* 1999). In contrast, after its decline in late 1992 in the Simpson Desert, the sandy inland mouse was present at very low densities until 1997, failing to increase in numbers after heavy rains over the summers of 1994/95 and 1996/97 (Dickman *et al.* 1999).

Notomys alexis (Thomas), the spinifex hopping-mouse, is found in sympatry with the former species in hummock grasslands. It is also a member of the Conilurini. This species has a body mass of 27-45 g, with a mean of 35 g (Breed 1983b), and is distinguished by elongated hind-limbs, a bipedal hopping gait, and a long, tufted tail used for balance (Watts and Aslin 1981). *Notomys alexis* is found across most of arid Australia, on sand-plains and dunes, the only exception being in south-western Queensland where the species is absent from isolated sand-dunes (Watts and Aslin 1974, Watts 1977). The species also occurs in tussock grasslands, acacia shrub-lands and open eucalypt forests (Burbidge *et al.* 1976, Watts and Aslin 1981). In the study area, it often forages in open microhabitat, far from spinifex tussocks, on crests and sides of dunes (M. Predavec unpublished data). It is quadrupedal when foraging, but bipedal when moving fast. The species is strictly nocturnal, and animals forage

less on full moon nights, although when active their microhabitat use is not influenced by levels of illumination (M. Predavec unpublished data).

Notomys alexis is a highly social species, living in common burrows in groups of up to ten individuals (Watts and Aslin 1981). The burrows are usually found on the crests or sides of dunes (M. Predavec unpublished data) and extend 1-2 m in depth. Like the sandy inland mouse, the spinifex hopping-mouse is well adapted to arid environments. It is able to survive independently of exogenous water, obtaining all its water requirements from the metabolism of carbohydrates, and from the moisture in its food (MacMillen and Lee 1967, 1970). Other physiological adaptations are the presence of few sweat glands in the skin, limiting water loss from the skin; high urine concentration, the highest so far recorded for a desert rodent (McNab 1979); and production of dry faeces (Watts and Aslin 1981). Females have four teats and litter size can vary between one and nine, averaging four (Watts and Aslin 1981). *Notomys alexis* is also an aseasonal breeder. The species becomes reproductively active from about three months, with females becoming sexually mature at 85 days (Watts and Aslin 1981). Gestation is 32-34 days and the time to weaning is a further 28 days (Smith *et al.* 1972, Happold 1976, Breed 1979). The normal oestrous cycle is 7-8 days, but its onset can be retarded if females are kept separated from males. In addition, the oestrous cycle can be extended or stopped through water deprivation (Breed 1975, 1976). In captivity, multiple matings have been observed in a single oestrous cycle (Breed 1990b, Breed and Washington 1991), but multiple paternity has not been observed (Breed and Adams 1992). There is some evidence of social suppression of reproduction at high densities of this species (Breed 1979). This species is also omnivorous (Murray *et al.* 1999). Seeds represent a large proportion of its diet, but other dietary items, such as invertebrates and green plant material, are also important at different periods of the year (Murray and Dickman 1994a).

Notomys alexis is also capable of long-range movements, with a significant increase in activity occurring during and after rainfall, compared to dry periods (Dickman *et al.* 1995). Low recapture rates have also been observed for this species, consequently, populations are often transient over short periods, with a high turnover of individuals. Eruptions of this species often coincide with those of *P. hermannsburgensis* (Predavec 1994a, b, Dickman *et al.* 1999). In the Simpson Desert, following the two eruptions of 1991 and 1992, the spinifex hopping-mouse apparently disappeared until 1997, after which it reappeared again at very low densities

(Dickman *et al*. 1999).

Another rodent species present in the study area is *Rattus villosissimus* (110-160 g); however it is rare and not a permanent inhabitant of hummock grasslands (Plomley 1972, Carstairs 1974). Following heavy rainfall, it may reach high densities in all arid habitats. *Pseudomys desertor* (25 g), *Notomys cervinus* (30 g), *Leggadina forresti* (20 g) and *Mus domesticus* (8-25 g), occur rarely in the study area.

As mentioned, these seven species, with the exclusion of *Leggadina forresti*, are periodically prone to population eruptions after heavy rainfall (Finlayson 1939, Plomley 1972, Newsome and Corbett 1975, Dickman *et al*. 1999).

CHAPTER 3: POPULATION DYNAMICS, ERUPTIONS AND RAINFALL

3.1. Introduction

Desert rodents in Australia show large population fluctuations (Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994a, b, Dickman *et al.* 1999) that are often linked strongly with rainfall. Population increases can be of two types (Plomley 1972, Newsome and Corbett 1975). The first is represented by plagues of non-permanent residents of the arid zone, such as *Rattus villosissimus*, that invade the arid zone as migratory hordes (Finlayson 1941, Plomley 1972, Carstairs 1974, 1976, Newsome and Corbett 1975, Predavec and Dickman 1994). The second type is represented by eruptions of permanent residents of the arid zone, such as *Pseudomys australis* (Finlayson 1941), *Pseudomys hermannsburgensis* (Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999), *Notomys cervinus* (Spencer and Gillen 1912), and *Notomys alexis* (Newsome and Corbett 1975, Masters 1993, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999). *Notomys mitchellii* (Sturt 1849) might also be included, although its distribution lies along the arid-semi-arid interface in southern Australia. These eruptions are usually interpreted as indirect responses by rodents to unusually large rainfall events, or more precisely as direct responses to increased food availability following heavy rain.

Several attempts have been made to describe and understand the causes triggering eruptions (Krebs 2002). For example, Predavec (1994b) found that a 40-fold increase in population numbers of *P. hermannsburgensis* and *N. alexis* after rain was due primarily to in situ reproduction, rather than to recruitment via immigration. A high turnover of individuals in populations of both species was also detected. Captures rates of the two species were correlated with an index of rainfall with a time-lag of four months, and also with an index of seed availability. Southgate and Masters (1996) found a similar trend for the same two species, with *P. hermannsburgensis* showing a 10-fold fluctuation in numbers over the study period, and *N. alexis* a rapid 5-fold increase, but taking a longer time to decline. They predicted that rodent populations would achieve densities of up to 10 individuals ha^{-1} or more in regions that receive three consecutive 6-month periods each with rainfall at 150% of the long-term average, followed by a dry period with rainfall equal to or less than 85% of the long-term annual average for two consecutive 12-month periods. Dickman *et al.* (1999) found that populations of *P. hermannsburgensis* and *N. alexis*

peaked six months after heavy rain in 1991 in the Simpson Desert, but failed to show any response to heavy rains in 1995. Responses to rains in early 1997 were similar to those in 1995, with only a slight response by *P. hermannsburgensis*. At Uluru increased capture rates of the two species were lagged at least 3-4 months after heavy rainfall, whereas in the Tanami Desert captures rates were not correlated with rainfall at all (Dickman *et al.* 1999).

These examples fail to show a clear and consistent pattern of response to rainfall by desert rodents (for other examples, see the reviews by Brown and Ernest 2002 and Krebs 2002). Clearly it is important to understand how much water is needed to trigger eruptions, during which period of the year it is most effective, and the optimal sequence and frequency of wet and dry periods. Even if rainfall is the triggering force that generates rodent eruptions, other factors may also be important in setting the beginning, the amplitude and length of such phenomena (e.g. Lima *et al.* 2002).

Soil nutrients when scarce or absent can inhibit plant growth even after heavy rains, and so inhibit the usual cascade process that rains initiate. This is true especially in Australia where soils are notoriously poor in phosphorus and nitrogen (Stafford Smith and Morton 1990, Latz 1996). Rain may also soften the ground, offering a better opportunity for burrowing animals to find shelter. On the other end, heavy rain can also drown animals in their burrows, diminishing the quantity of usable shelters (Woolley 1984, Brown and Ernest 2002).

Other factors that can modify population trends include predation (e.g. Lima *et al.* 2002), competition and the presence and accessibility of refugia (Morton *et al.* 1995) where rodents can survive long droughts or escape from predators. These factors have been discussed earlier, and are therefore not considered further here.

In this chapter I use pattern analyses to describe changes in numbers (or, rather, capture rates) of *P. hermannsburgensis* and *N. alexis* in relation to rainfall (Bradley and Maurer 1971, Dunigan *et al.* 1980, Brown and Zeng 1989), in the Simpson Desert. Trapping took place at twelve different sites over periods of 4-12 years, thus offering the chance to compare population patterns on a broad spatial scale as well as on a long temporal scale which covered both extremely wet and dry periods.

3.2. Materials and Methods

3.2.1. Trapping

Captures of the two study species were made between March 1990 and December 2001 at twelve sites in the Simpson Desert, western Queensland. The sites were Carlo, Cravens Peak, Ethabuka Station, Field River North, Field River South, Koonamuka East, Koonamuka West, Naibar, Plum Pudding, South, Tobermorey East, and Tobermorey West (Figure 2.1). Sites were established at different times between 1990 and 1997, so capture durations are variable. My contribution to the trapping data was from 1998-2001, with earlier records provided by C. R. Dickman (*pers. comm.*).

Animals were trapped in pitfall traps (PVC pipe, 16 cm diameter, 60 cm deep). In order to increase trapping efficiency, each trap was equipped with a 5 m flywire drift fence (Friend *et al.* 1989). Traps were set in grids, with each grid consisting of 36 pitfall traps in a 6 x 6 quadrat. Each trap station was placed 20 m apart, and each grid covered 1.0 ha. Grids were spaced 0.5-2.0 km apart within each study site, with sites containing 2-12 grids each. Grids were positioned on dune sides, with the first trapline running along the crest (Predavec 2000).

Trapping was usually conducted every 2-3 months, although longer or shorter intervals between trapping sessions occurred. Traps were usually opened for three consecutive nights per site, but varied from one to six nights depending on weather and other conditions. Traps were checked once or twice a day. Each captured animal was weighed, sexed, marked using a unique combination of toe clipping (until 1993) and ear clipping (1993-2001), and checked for reproductive condition. It was then released at the point of capture.

Because within-trip recapture rates were low (usually < 10%), it was impossible to use population models (mark-release-recapture techniques) to estimate population sizes. Instead, raw trapping data, expressed as either mean captures per gridnight (number of captures on night 1/number of open grids on night 1) or mean captures per trapnight (number of captures on night 1/ number of open traps on night 1), excluding within-trip recaptures, were used to produce population indices. Standard errors were calculated using grids as replicates (Dickman *et al.* 1999). Trapping usually took place within a week of the new moon, to reduce variability in foraging behaviour and activity due to potential

sensitivity to predation risk (Kotler *et al.* 1991, Predavec 1994a, Predavec and Dickman 1994).

Reproductive condition of female rodents was categorised as juvenile (vagina closed and small body mass); non-parous (nipples inconspicuous or tiny, but adult body mass); parous (nipples visible and enlarged, vagina closed, animal not currently reproductively active); reproductively active: mated (just mated with the vagina open, bruised or bloody, with or without a mating plug), pregnant (abdomen swollen, embryos palpable and hair around nipples reduced), lactating (nipples very visible and swollen, no embryos present, milk secretions). The boundary between juvenile and adult status was based on the minimum body mass of females known to be non-pregnant adults (non-pregnant parous or just- mated individuals). This delineation was 9 g for *P. hermannsburgensis* and 20 g for *N. alexis*; thus non-parous *P. hermannsburgensis* < 9 g and *N. alexis* < 20 g were defined as juvenile (Predavec 1994a, Mahon 1999, S. Ricci unpublished data). Similar minimum body masses for adults have been reported by Breed (1979, 1982).

Male rodents were recorded as juvenile or non-scrotal (testes inguinal); semi-scrotal (testes partly descended but not in a fully distended scrotum); and scrotal (scrotum very conspicuous with testes fully distended). Juvenile status for males was decided on the basis of their breeding condition, not on their mass (Predavec 1994a).

3.2.2. Rainfall

The two nearest long-term weather stations were used to collect data on rainfall over long periods of time. Marion Downs station (23°21'54"S, 139°39'06"E) is 120 km east of Ethabuka Station. Average annual rainfall for this station calculated on records from 1913 to 2001 is 201 mm. Data on rainfall from Marion Downs show a good agreement with unofficial rainfall records from Ethabuka homestead, 15 km south of the Ethabuka Station site (Dickman *et al.* 1999). Monthly rainfall records from 1913 to 2001 for Marion Downs were used to calculate long-term means. A second long-term weather station is Glenormiston (22°55' S, 138°49' E). Records from this station were compared initially with those from limited on-site data, but not further used (see below).

In addition to the long-term weather station, other on-site weather stations were established at the twelve sites over the study period. Measurements of rainfall (and temperature) were recorded hourly, stored in a data-logger and the information down-loaded during routine mammal trapping at each sampling station. The first rainfall records registered on-site were: in late July 1995 at Carlo, in May 1995 at Cravens Peak, in May

1995 at Ethabuka Station, in October 1997 at Field River North, in May 1995 at Field River South, in June 1997 at Koonamuka Swamp East, in July 1997 at Koonamuka Swamp West, in December 1997 at Naibar, in June 1997 at Plum Pudding, in June 1998 at South, in August 1998 at Tobermorey East and West. Such records were used when available as they were more accurate than those from the two long-term stations.

Monthly rainfall records from each on-site station were correlated separately with the rainfall records from Marion Downs and Glenormiston, and with the average rainfall of these two long-term weather stations. Pearson product-moment correlations (Sokal and Rohlf 1995) were used for all correlations. In general, the results showed that the strongest site-specific associations were with Marion Downs rainfall records or with Marion-Glenormiston averages (Table 3.1).

Table 3.1. Correlation coefficients for monthly rainfall records of on-site weather stations with records from the two long-term weather stations and from the averages of the two long-term weather stations. *P* values are given for the correlation coefficients shown in bold font.

Site	Glenormiston	Average (Glenormiston-Marion Downs)	Marion Downs	*P*
Carlo	0.651	0.737	**0.770**	<0.001
Cravens Peak	0.773	**0.817**	0.807	<0.001
Ethabuka	0.735	0.800	**0.811**	<0.001
Field River North	0.774	0.838	**0.847**	<0.001
Field River South	0.444	**0.462**	0.450	<0.01
Koonamuka Swamp East	0.720	0.808	**0.838**	<0.001
Koonamuka Swamp West	0.744	0.820	**0.841**	<0.001
Naibar	0.782	**0.829**	0.825	<0.001
Plum Pudding	0.739	0.788	**0.788**	<0.001
South	0.775	0.880	**0.922**	<0.001
Tobermorey East	0.627	0.730	**0.778**	<0.001
Tobermorey West	0.836	**0.860**	0.838	<0.001

Consequently, Marion Downs data and the average between Marion Downs and Glenormiston data were used together with data from the on-site weather stations in the pattern analyses of this chapter.

3.2.3. Patterns of rainfall and species abundances

Graphical comparisons between rainfall and abundances of the two species were used initially to detect possible patterns. A more quantitative analysis was carried out subsequently, correlating capture rates with rainfall.

Previous studies (Berndtsson 1987, Sutherland *et al.* 1991, Masters 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999) have presented a variety of ways to compare rainfall with an index of animal abundance. For my study, I chose to express rainfall as the cumulative monthly rainfall residual (CDMR (exp)) modified according to Predavec (1994b) and Dickman *et al.* (1999) and using the Marion Downs records to obtain long-term averages. This choice was motivated by the need to accommodate the CDMR function (Berndtsson 1987, Sutherland *et al.* 1991) for the skewed distribution of rainfall typical of arid Australia. The CDMR function is likely to be insensitive to periods of droughts following periods of exceptionally high rainfall (Sutherland *et al.* 1991). Even more important for this study was the necessity to estimate rainfall-induced resources in order to map the likely availability of food such as seeds. To address these two issues an exponential decay function was fitted to CDMR values to predict the probable decline of rain-induced resources with time from the rain event. Data on the rate of decline of seed biomass in sand were used to estimate this decline, at Ethabuka Station, during a period of low but average rainfall that followed heavy rain in early 1992 (Predavec 1994b); these data showed a decay rate of approximately 20% per month (i.e. seed density decreased by 20% per month).

The CDMR corrected to take this decay rate into account is

$$CDMR(exp)(n+1) = (CDMR(exp)(n) \times 0.8) + DMR\ (n+1)$$

where CDMR(exp)(n) is the modified cumulative deviation from mean monthly rainfall for month n, and DMR(n+1) is the deviation from mean monthly rainfall for month n+1. Residual values were multiplied by 0.8, so that the effects of heavy rain decayed exponentially with time.

Correction of the CDMR is based on some assumptions (e.g. that only seeds are important in rodent diets) that are unlikely to describe the real decline of rain-induced resources. Nevertheless, this function is more realistic in describing wet and dry periods than the unmodified CDMR, which assumes a constant availability of resources after a large rainfall event.

Captures per trapnight of the two species were correlated with the modified CDMR values for the same months. In order to accommodate likely lag effects, capture rates were also correlated with the modified CDMR values for each of the previous 12 months. Pearson product-moment correlation coefficients (Sokal and Rohlf 1995) were used for all correlations. *P*-values were adjusted using the Dunn-Sidak correction for multiple

comparisons (Sokal and Rohlf 1995). Captures per trapnight were used in the correlations because they are likely to represent a more precise index of abundance than captures per gridnight, since traps were sometimes closed within trips due to ant infestation or repairs. However, in the graphical presentations captures per gridnight are shown because of the difficulties of calculating standard errors for captures per trapnight. Graphical comparisons showed that differences in patterns between the two methodologies were minimal. In addition, graphical results depict capture rates of the two species with unmodified rainfall each month rather than with the modified CDMR, to provide a ready depiction of the actual rainfall pattern.

The use of successive sampling periods for comparing rodent capture rates with rainfall creates problems of statistical independence and therefore is not completely appropriate for correlation analysis. However, I follow previous studies (Masters 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999) in using this approach to identify patterns in the data, and not to test specific hypotheses.

Finally, correlations between the two species at each study site were computed to detect the degree of concordance in their responses to rainfall (Table 3.2). Pearson product-moment correlation coefficients (Sokal and Rohlf 1995) were again used for all correlations.

Table 3.2. Correlation coefficients, *r* for the comparison of capture rates of *N. alexis* with capture rates of *P. hermannsburgensis* in each study site. df = degrees of freedom, *P*-values presented, n.s.=non significant.

Site	*r*	df	*P*
Carlo	0.637	27	<0.001
Cravens Peak	0.818	29	<0.001
Ethabuka	0.781	73	<0.001
Field River North	0.925	19	<0.001
Field River South	0.573	31	<0.01
Koonamuka Swamp East	0.765	21	<0.001
Koonamuka Swamp West	0.909	20	<0.001
Naibar	0.369	18	n.s.
Plum Pudding	0.572	21	<0.01
South	0.188	10	n.s.
Tobermorey East	0.897	16	<0.001
Tobermorey West	0.927	13	<0.001

3.3. Results

3.3.1. Rainfall

The study period covered twelve years, from March 1990 to December 2001. Over this period, exceptionally high rainfalls and minor droughts were recorded. The wettest years, using the data from Marion Downs and Glenormiston, were 1991 with respectively 513.7 mm and 665.4 mm of rain, and 2000 with 680.1 mm and 632.9 mm of rain. These records are well above the annual averages for the last 88 years (201 mm for Marion Downs and 218 mm for Glenormiston). Prior to 1991, there was a period of three years with below average annual rainfall.

Usually the wettest months based on Marion Downs data have been January, with a total monthly average 39.6 mm, and February with 38.8 mm, followed by December with 24.6 mm. The driest months have been August with 4 mm of rain and September with 6.2 mm. Other years with above average rainfall were 1992, 1995, 1997 and 2000 and again most of the rain fell during the summer months. Years of below average rainfall were 1990, 1994, 1996 and 1998. The remaining years were near average. Similar patterns were recorded for on-site weather stations. The wettest year was 2000, with the annual rainfall at all twelve sites being well above the annual average calculated on Marion Downs data. Overall, the site with the highest monthly average was Ethabuka Station with 44.1 mm of rain, about 1.6 times higher than the second wettest site (Naibar), and 3.8 times higher then the driest site (South). In general, the months of this study with most rain were February, April and December. In contrast, the driest months were in winter, from May to September. Such rainy events were often followed by production of seeds by desert plants, especially *Triodia basedowii*, which produced a vast amount of seed within several weeks across the study area (C.R. Dickman *pers. comm.*, P.S. Mahon *pers. comm.*, S. Ricci *pers. obs.*).

3.3.2. Rodent dynamics

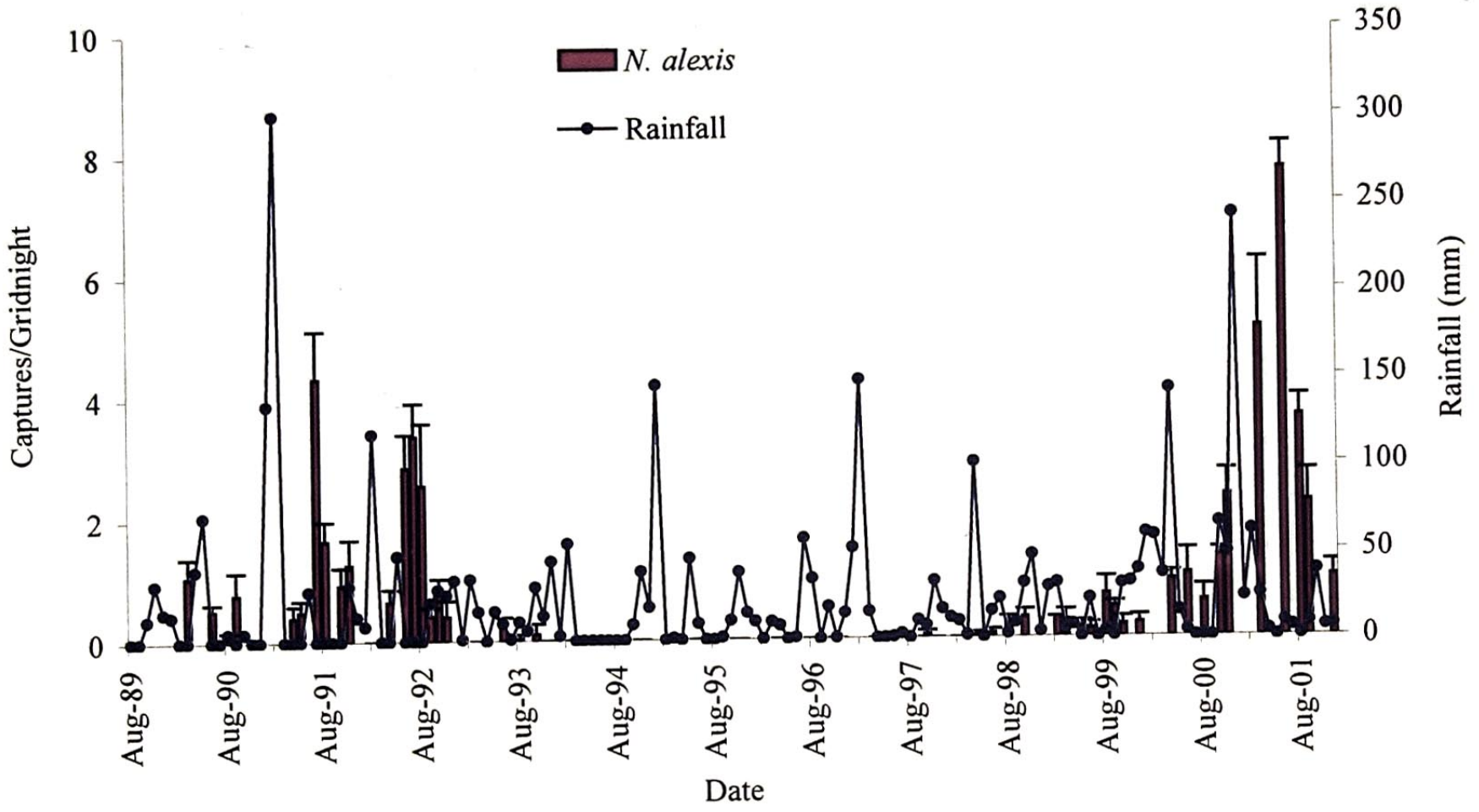
Over the study period, different numbers of trips were made to each site. At Carlo small mammal populations were censused on 29 occasions (from June 1994 to December 2001), at Cravens Peak on 31 occasions (from May 1995 to December 2001), at Ethabuka on 75 occasions (from March 1990 to December 2001), at Field River North on 21 occasions (from June 1997 to December 2001), at Field River South on 33 occasions (from

April 1995 to December 2001), at Koonamuka Swamp East on 23 occasions (from May 1996 to December 2001), at Koonamuka Swamp West on 22 occasions (from June 1997 to December 2001), at Naibar on 20 occasions (from May 1996 to December 2001), at Plum Pudding on 23 occasions (from March 1996 to December 2001), at South on 12 occasions (from March 1996 to December 2001), at Tobermorey East on 18 occasions (from April 1997 to December 2001), and at Tobermorey West on 15 occasions (from October 1998 to December 2001).

Figures 3.1 to 3.12 show captures per gridnight (+ SE) for the two species at each site, plotted with on-site rainfall for the period of the study. For each site rainfall data are presented starting one year before the first trapping session. At Ethabuka where twelve years of records are available, dramatic fluctuations of the two rodent species are evident over the study period (Figure 3.1). The conspicuous rainfall event of February 1991 was followed by an increase in capture rates to almost five times those measured before the rain for both species, with peaks in August 1991. The two species declined sharply over the subsequent five months. Another eruption occurred after the smaller rains of February 1992. *P. hermannsburgensis* peaked at lower levels than the previous year in July 1992, while *N. alexis* peaked to similar levels as the previous year in June 1992, although less rain fell than in the previous summer. As in 1991, the two species declined shortly after these winter peaks in 1992. Following very low capture rates in early 1993, *N. alexis* virtually disappeared from the study area for over four years, from October 1993 until March 1998. No response was observed to major rainfall events in January 1995 and February 1997. However, heavy rains in April 2000 and January 2001 triggered a new eruption of *N. alexis* that peaked in June 2001 with a magnitude almost 1.8 times greater than the one recorded ten years before. By December 2001 the population had declined some 7.5-fold. Capture rates of *P. hermannsburgensis* capture rates remained constantly very low from March 1993 to July 1997 after which, in September and October 1997, a small response to the rain of February 1997 was shown (Figure 3.1). A second small response in October 1998 followed the rainy event of April 1998. The rains in April 2000 and January 2001 were followed by a new eruption that peaked in March 2001, although this did not achieve the same magnitude as the eruption in July 1991. The population declined rapidly within six months of its peak.

Similar patterns in population dynamics are shown at the other study sites (Figures 3.2-3.12). In general, following periods of low abundance or even absence between 1995 and

a.



b.

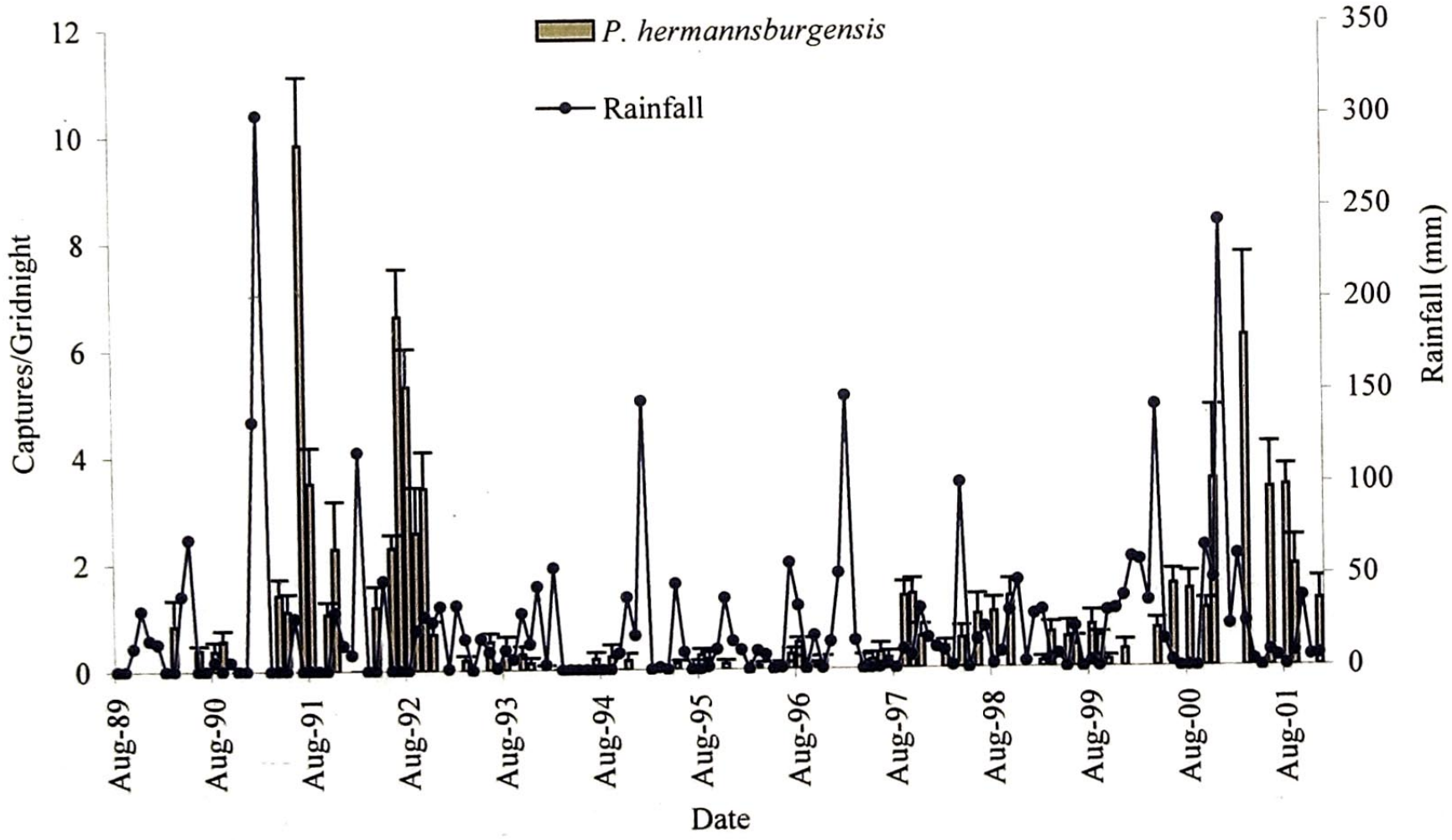
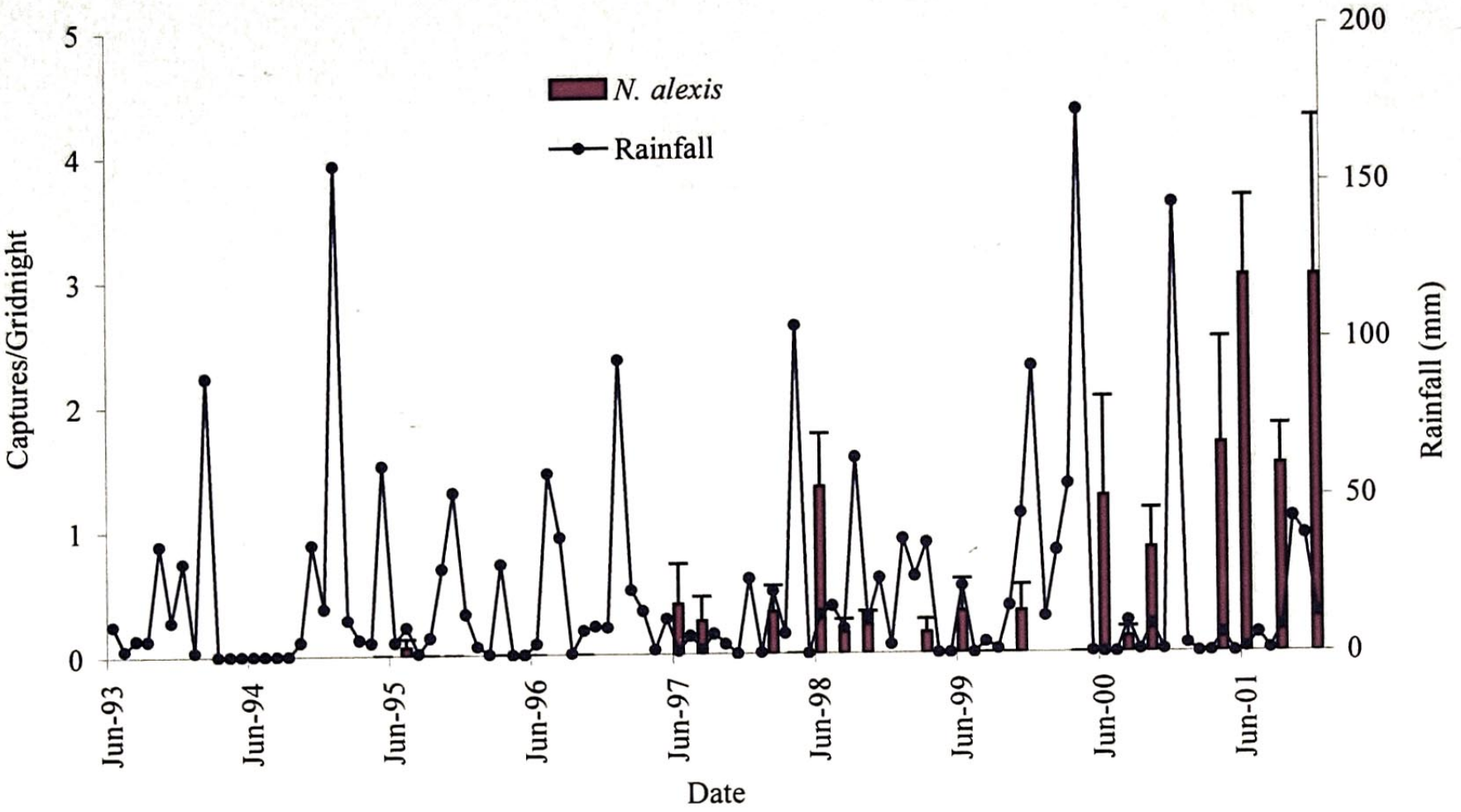


Figure 3.1. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* **b**) plotted with monthly rainfall totals for Ethabuka Station site. Within-trip recaptures are not included.

a.



b.

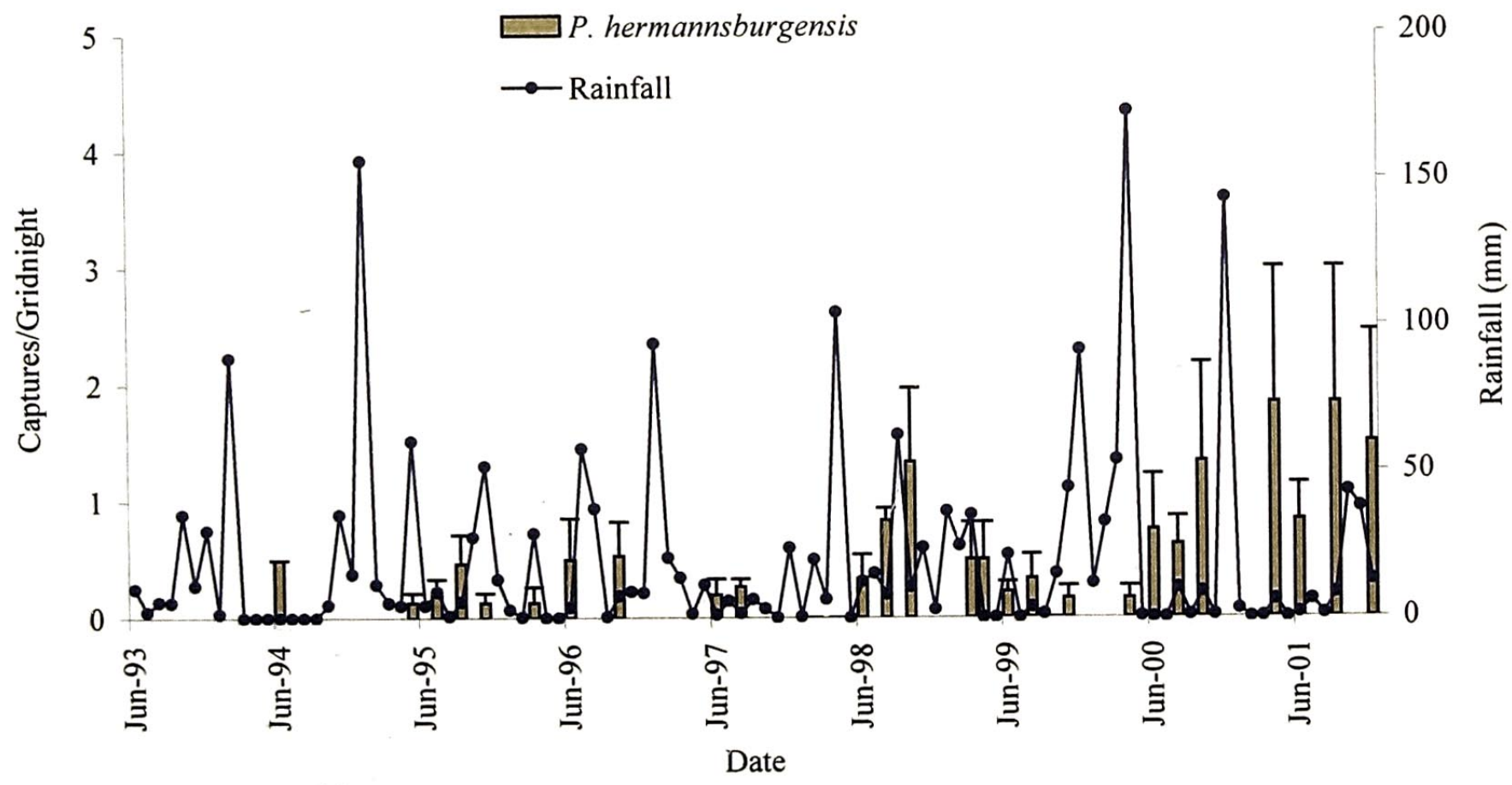
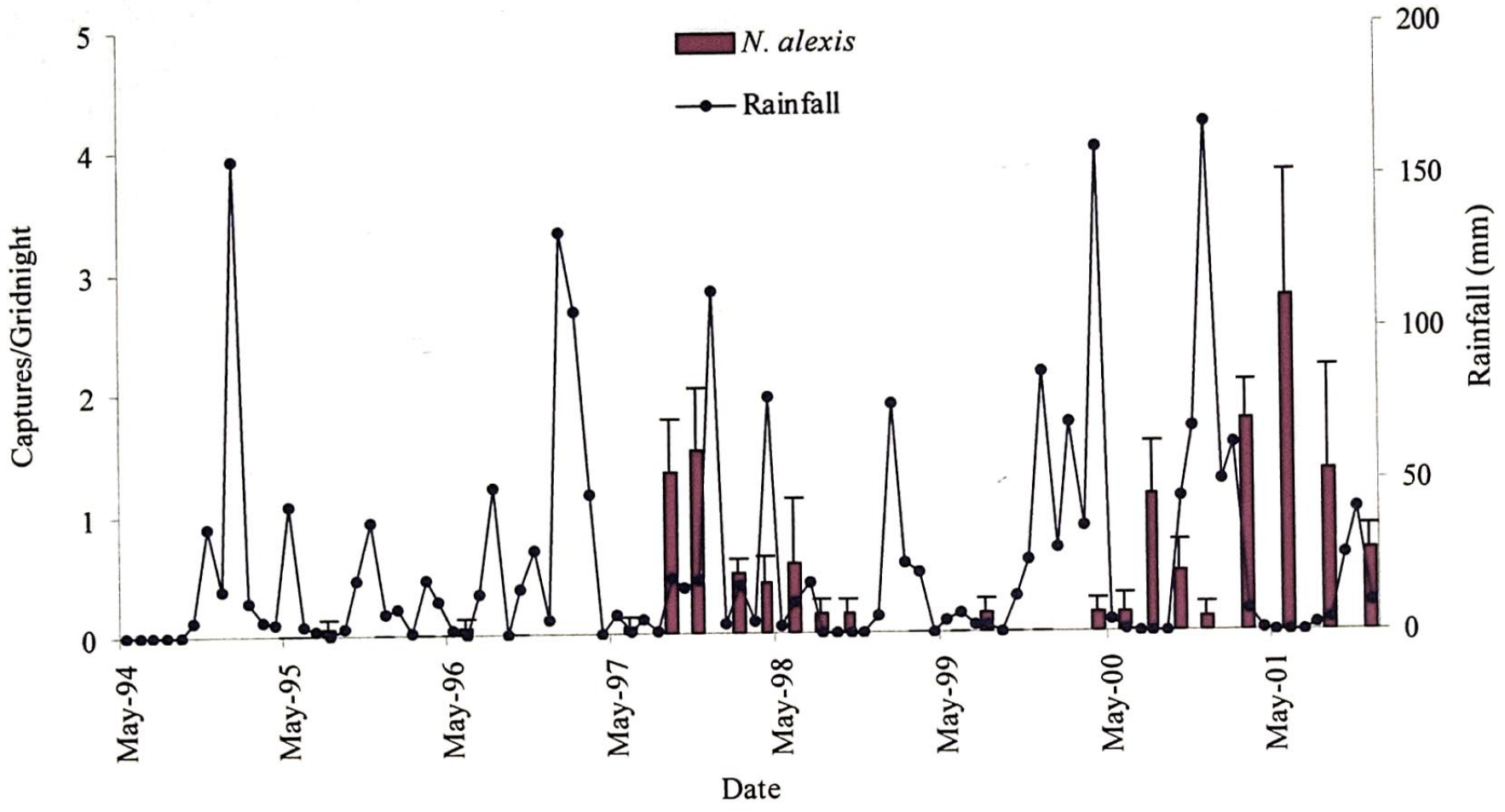


Figure 3.2. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Carlo site. Within-trip recaptures are not included.

a.



b.

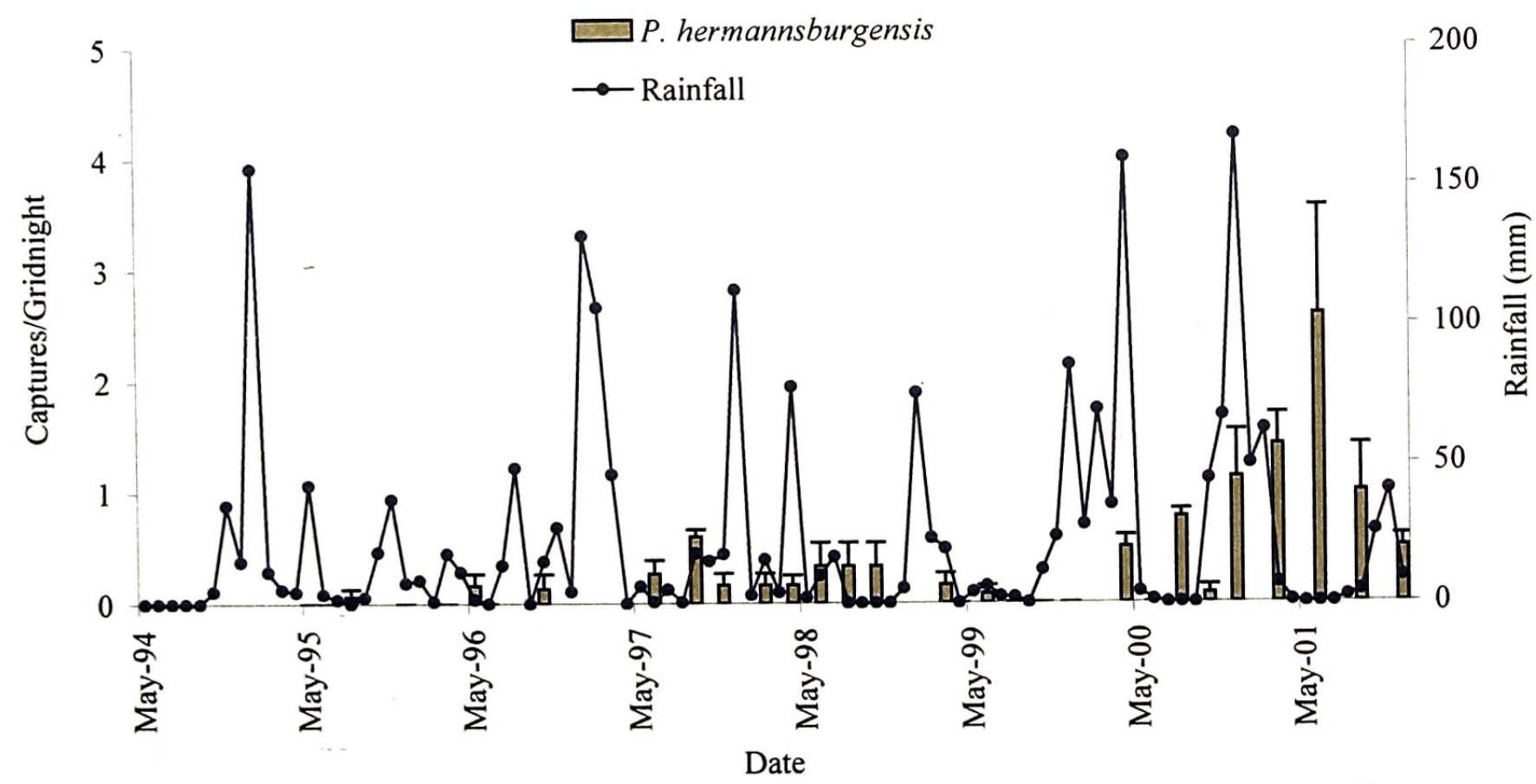
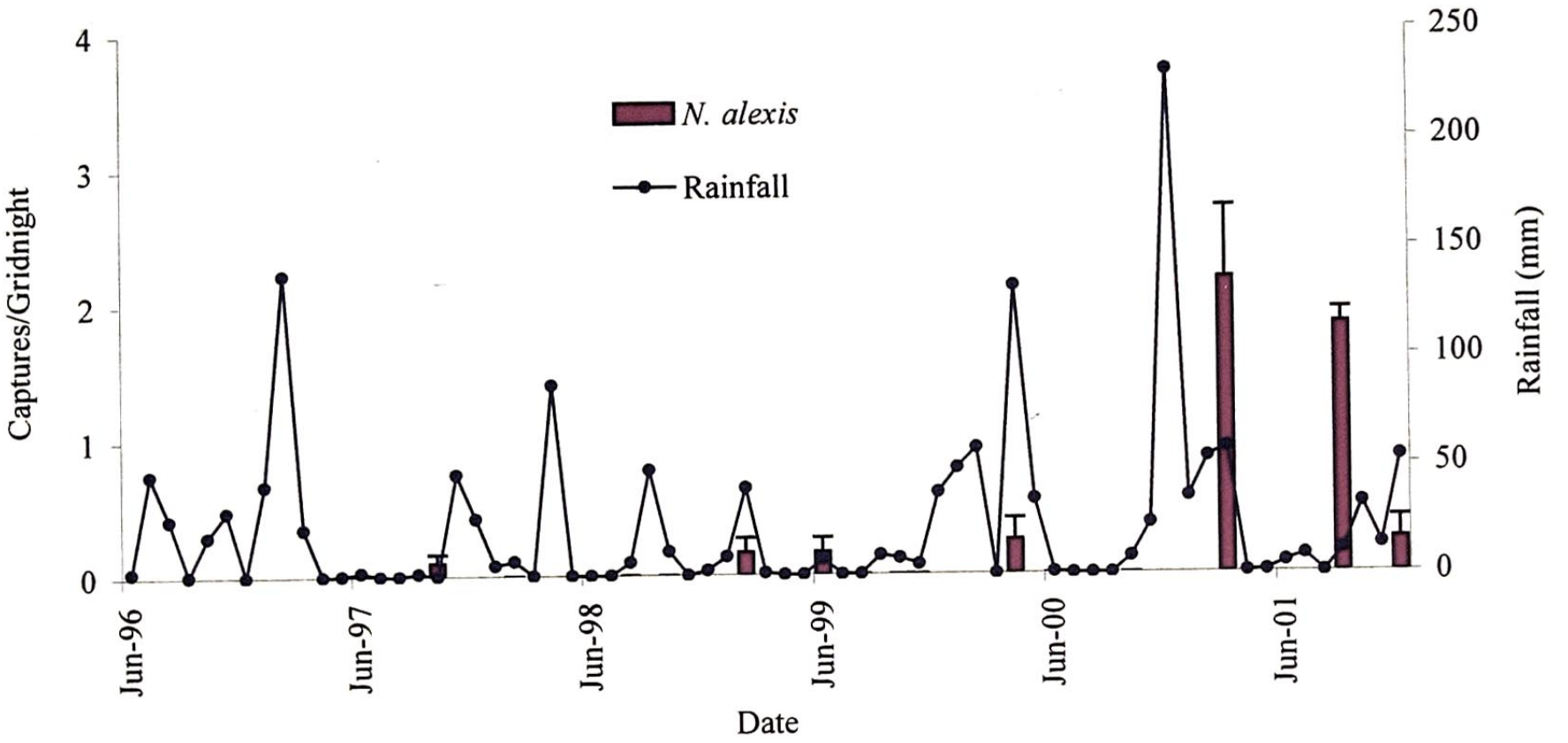


Figure 3.3. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Cravens Peak site. Within-trip recaptures are not included.

a.



b.

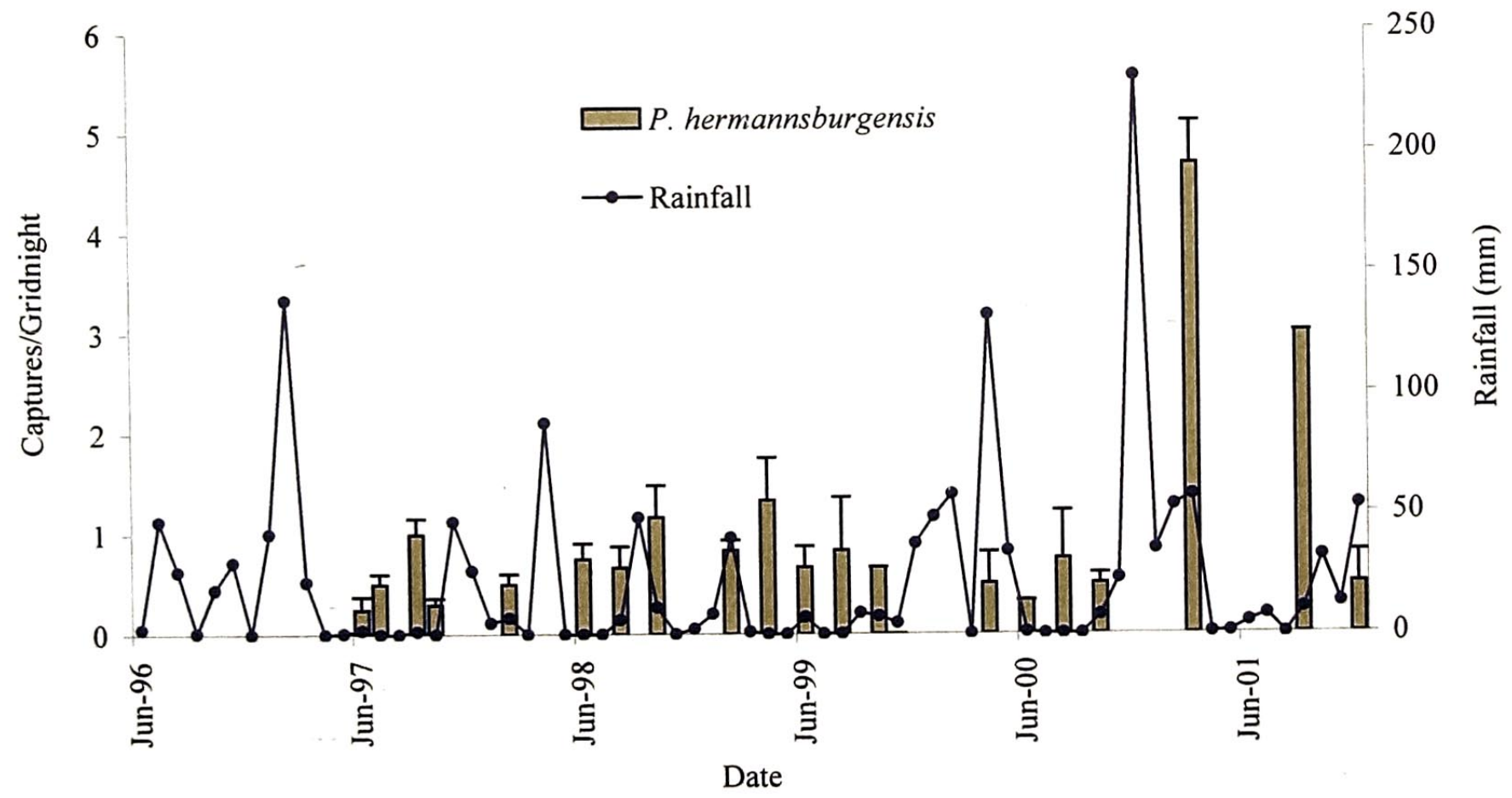
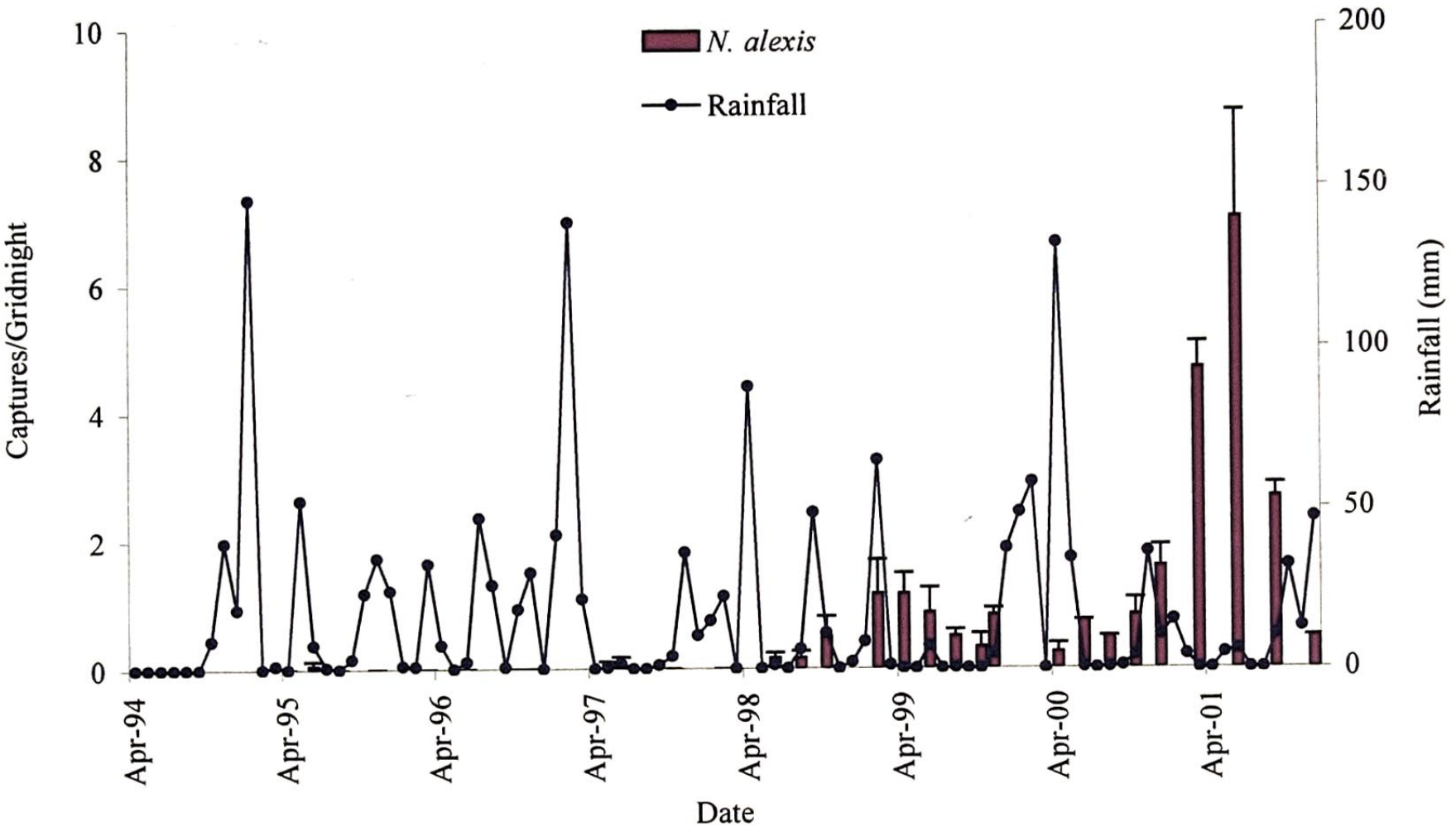


Figure 3.4. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Field River North site. Within-trip recaptures are not included.

a.



b.

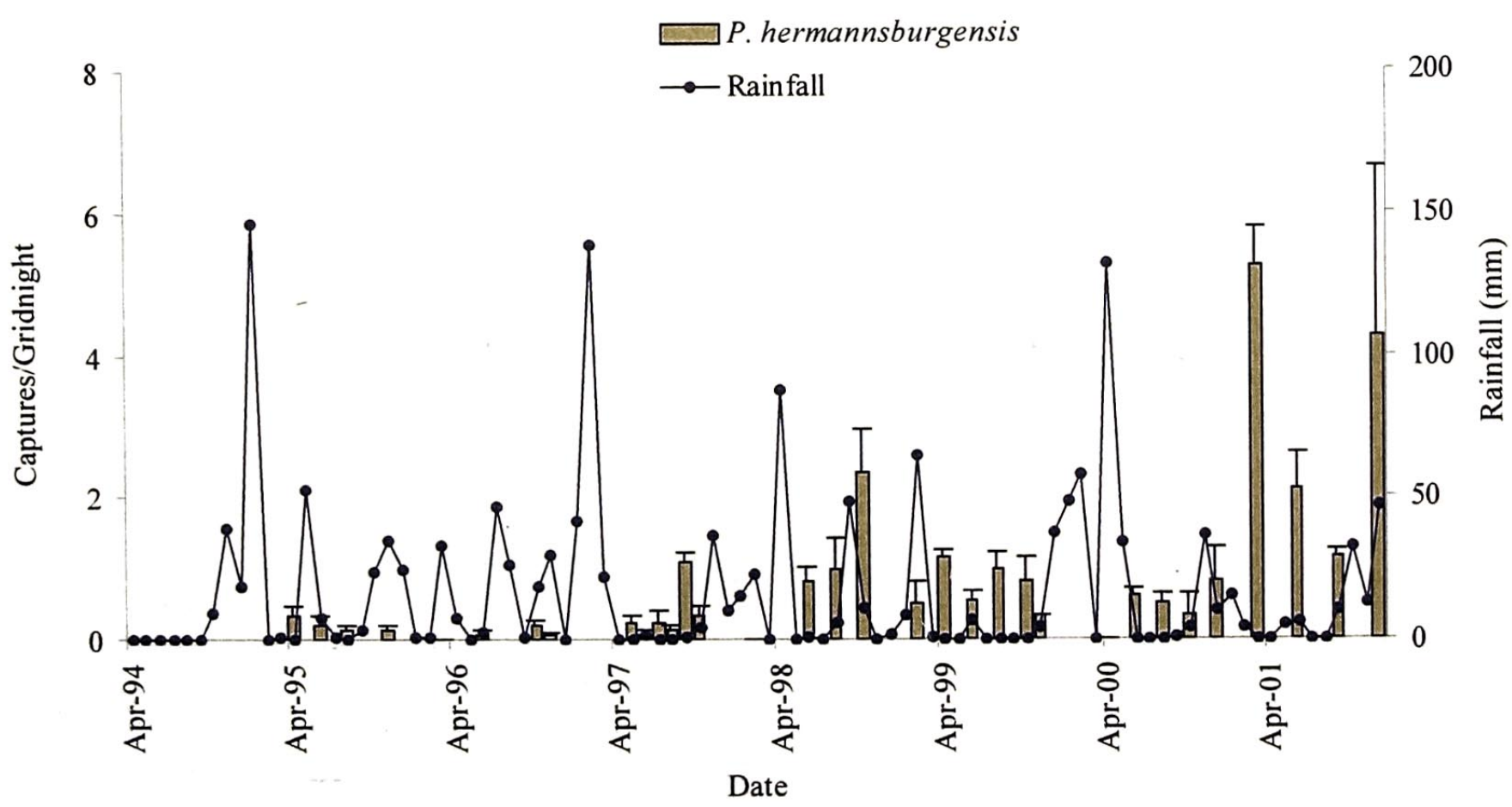
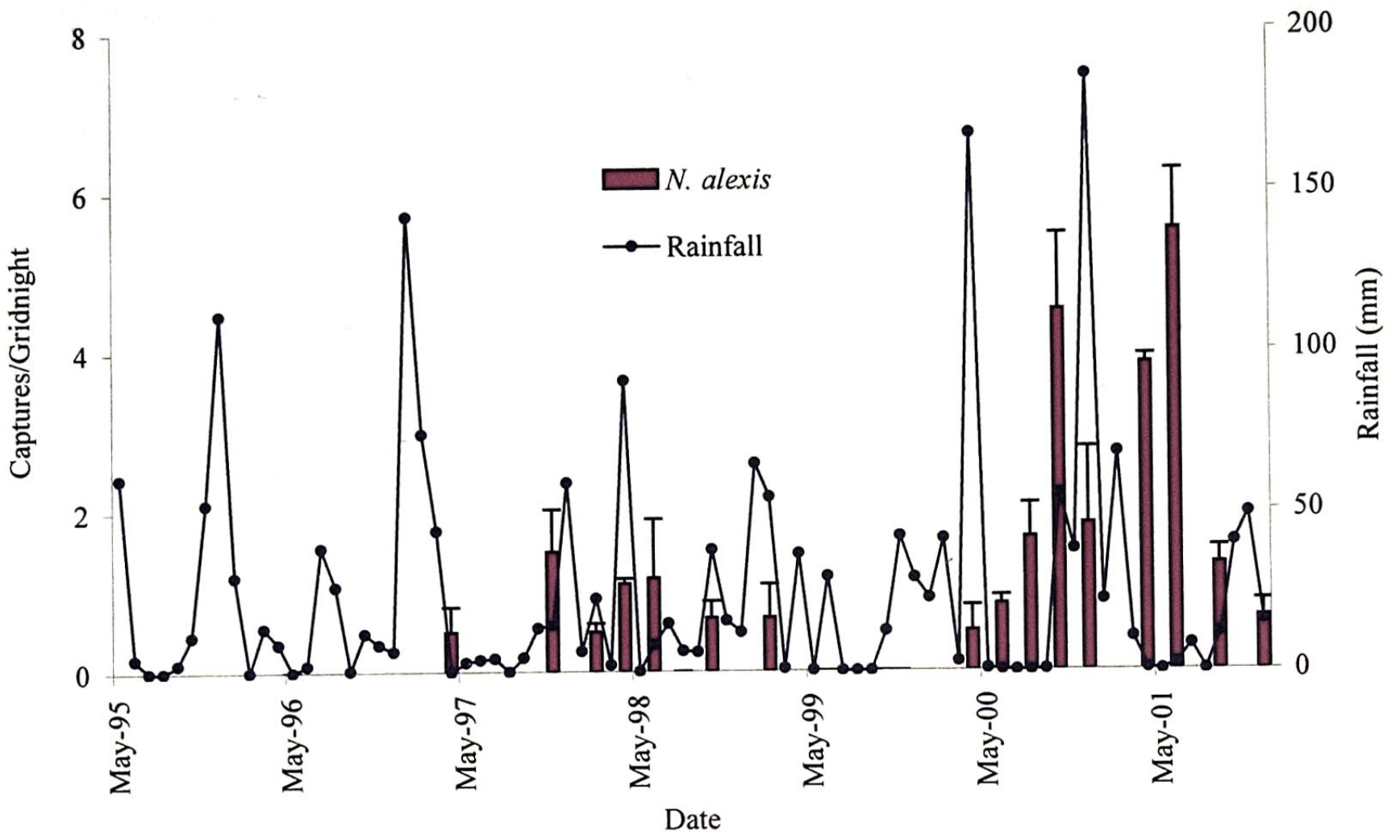


Figure 3.5. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Field River South site. Within-trip recaptures are not included.

a.



b.

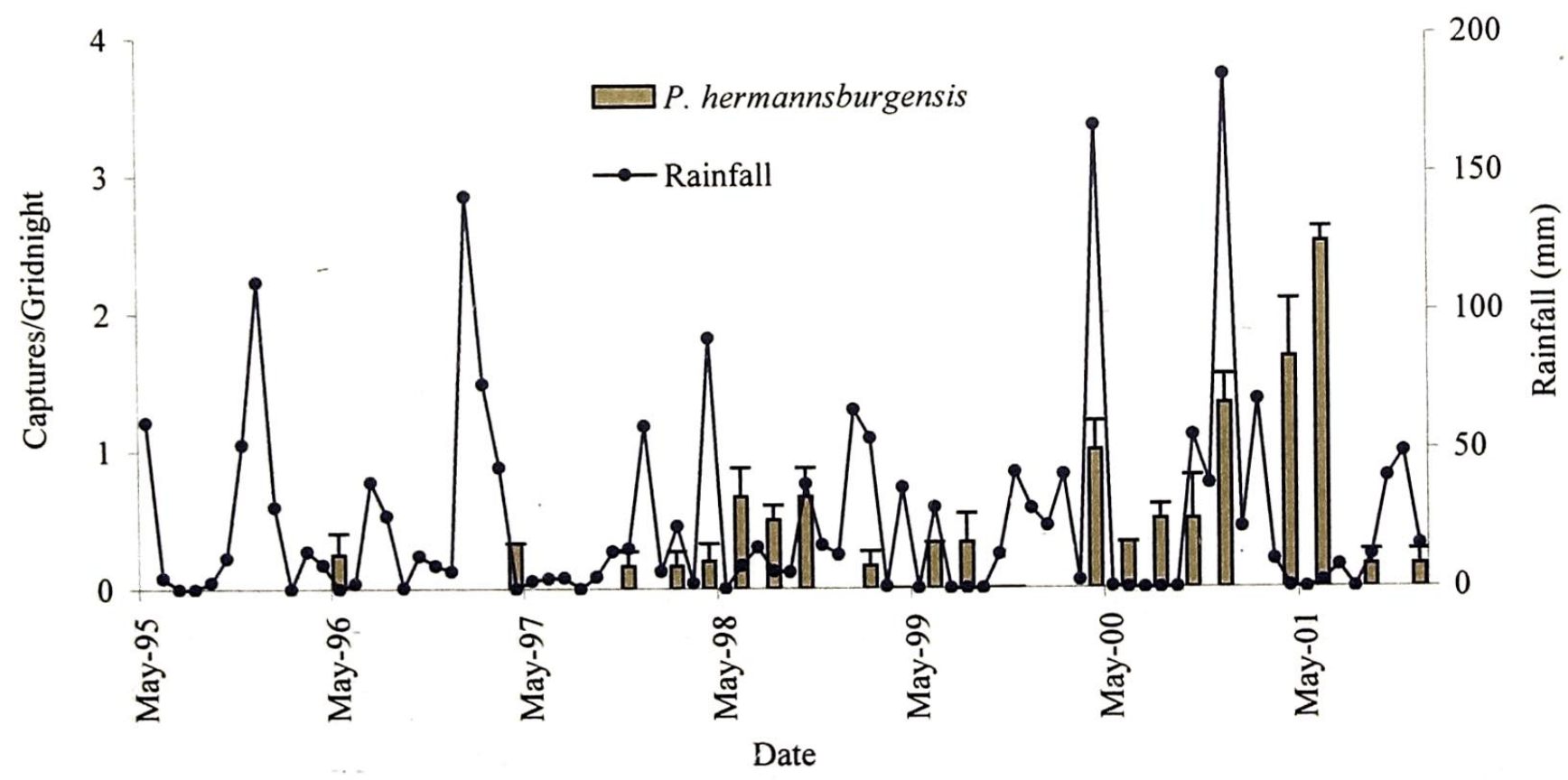
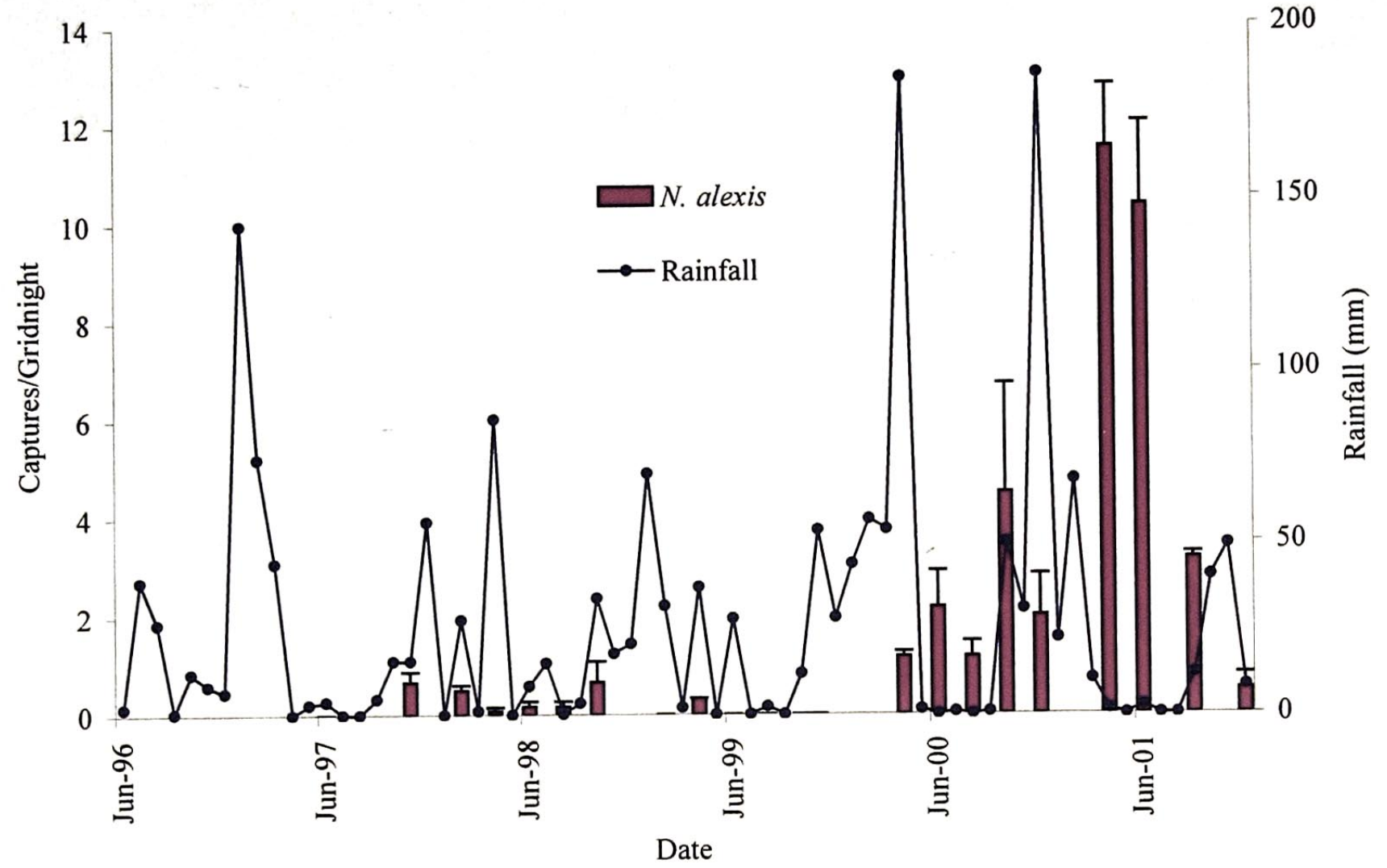


Figure 3.6. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Koonamuka Swamp East site. Within-trip recaptures are not included.

a.



b.

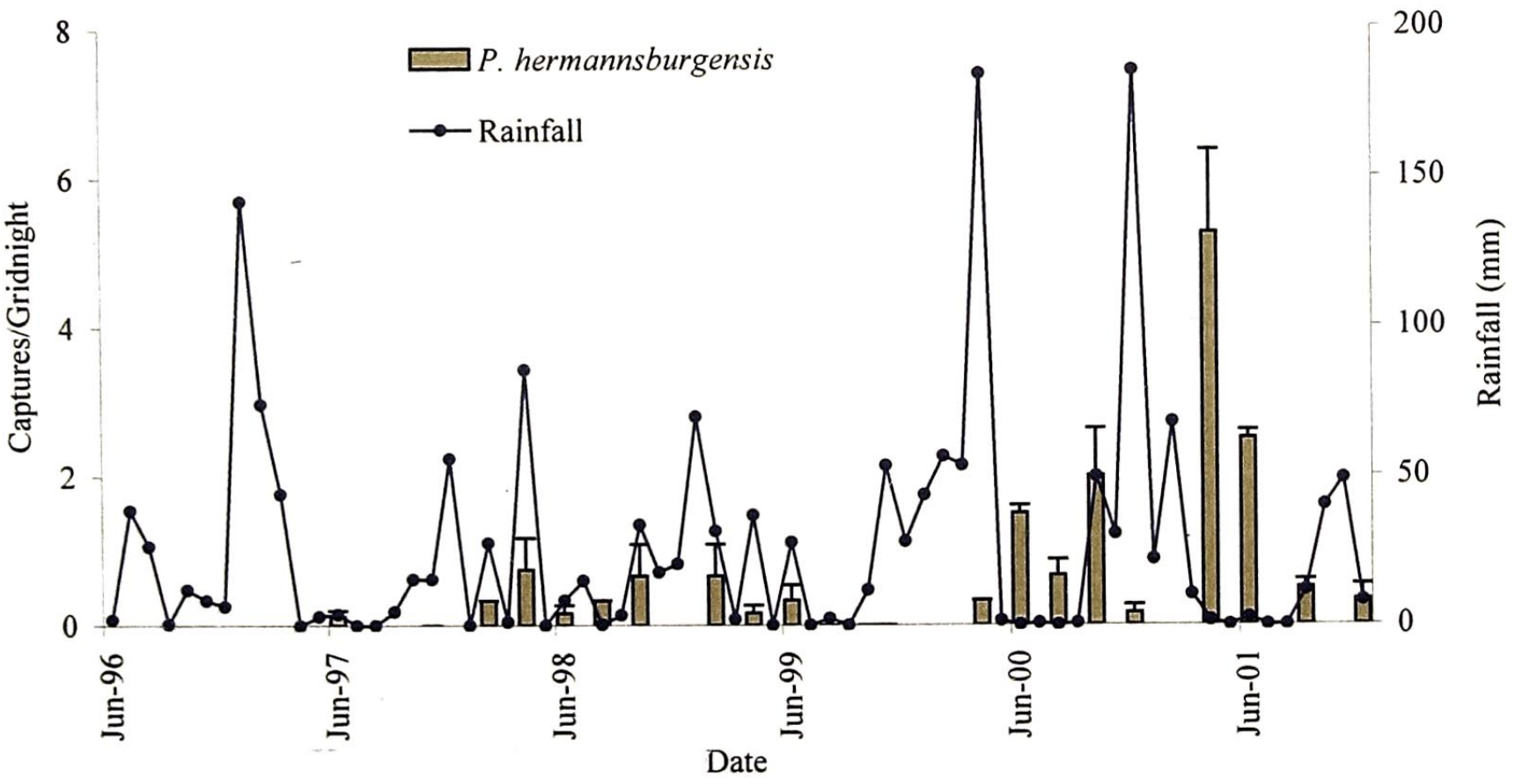
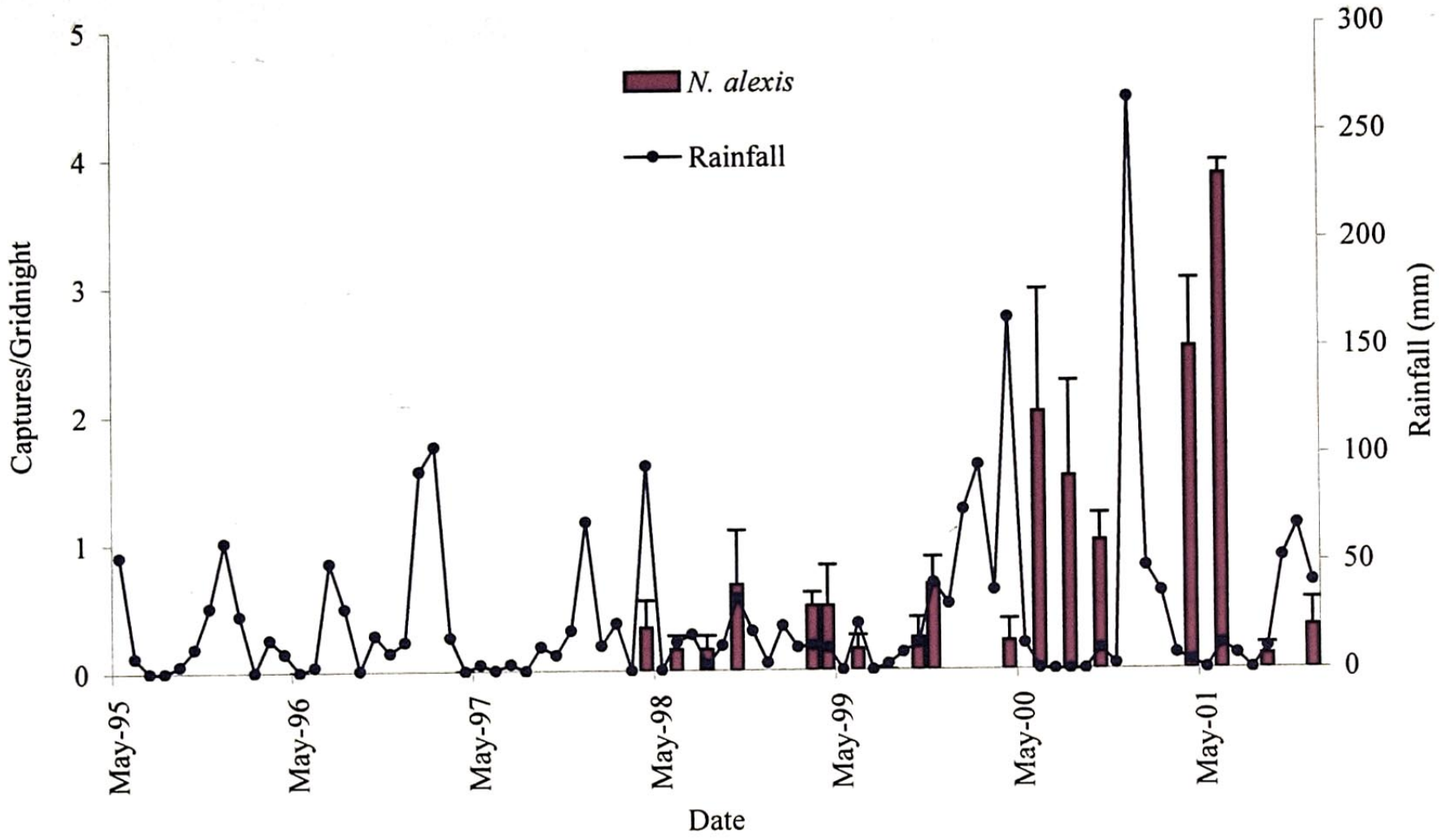


Figure 3.7. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Koonamuka Swamp West site. Within-trip recaptures are not included.

a.



b.

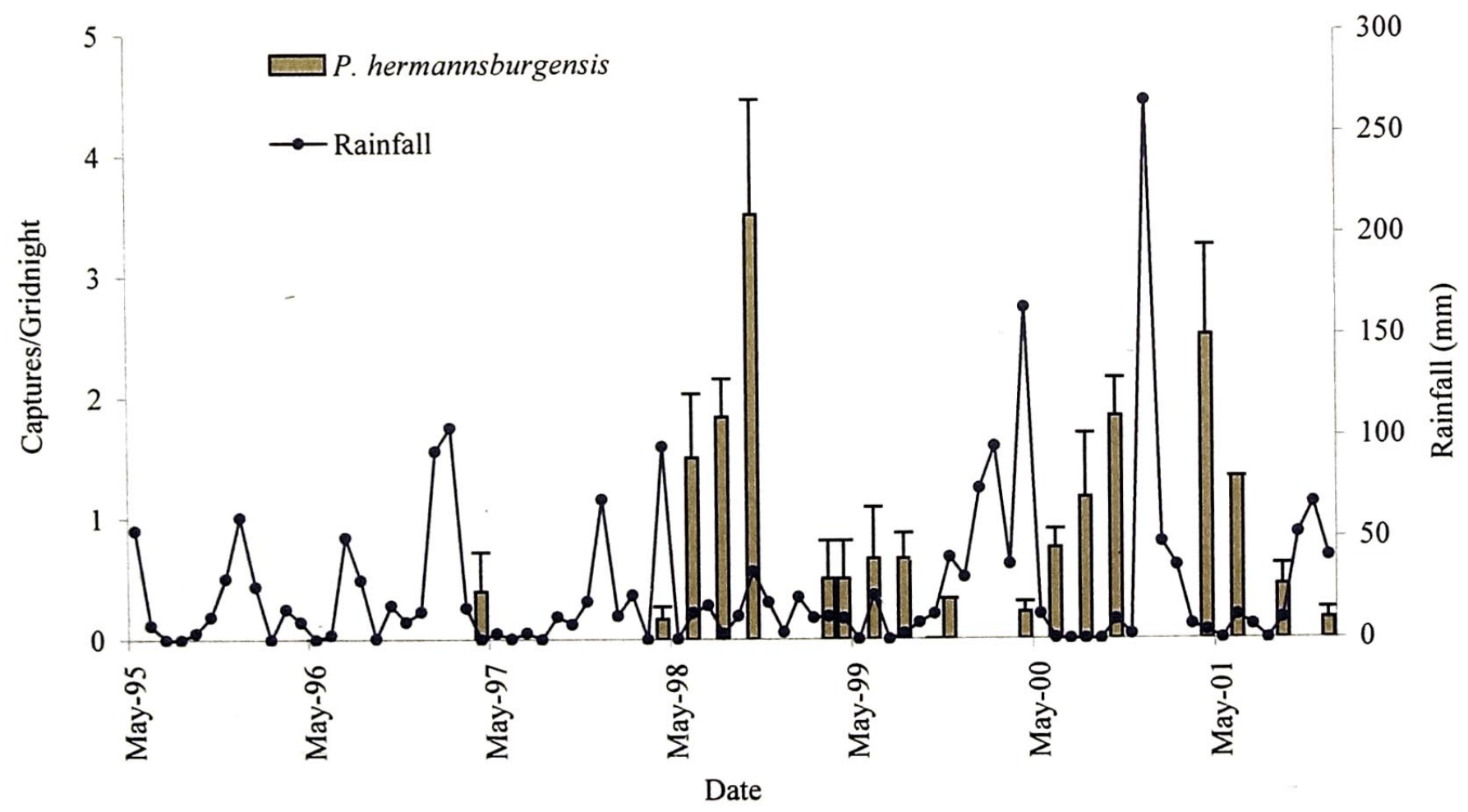
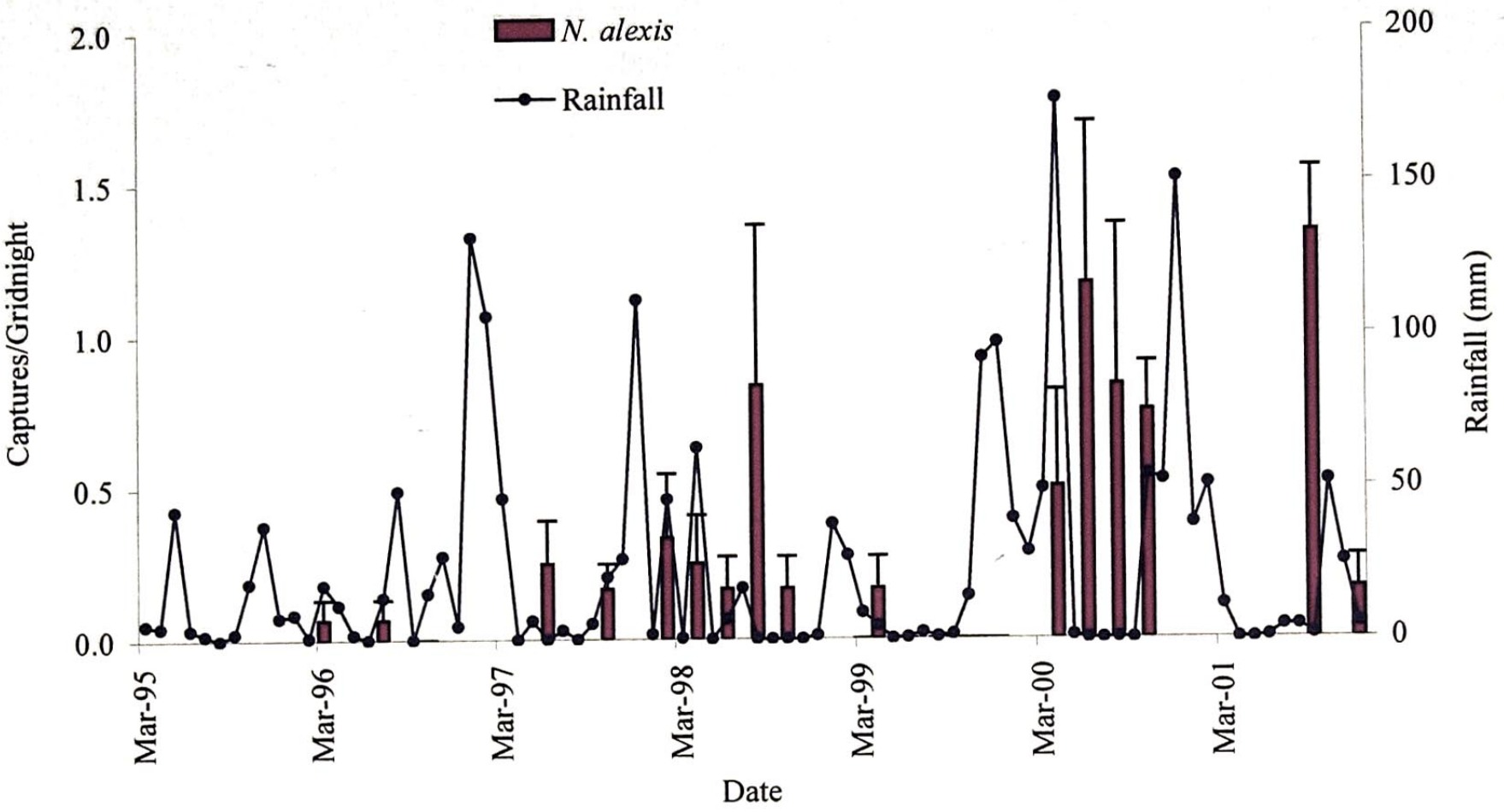


Figure 3.8. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Naibar site. Within-trip recaptures are not included.

a.



b.

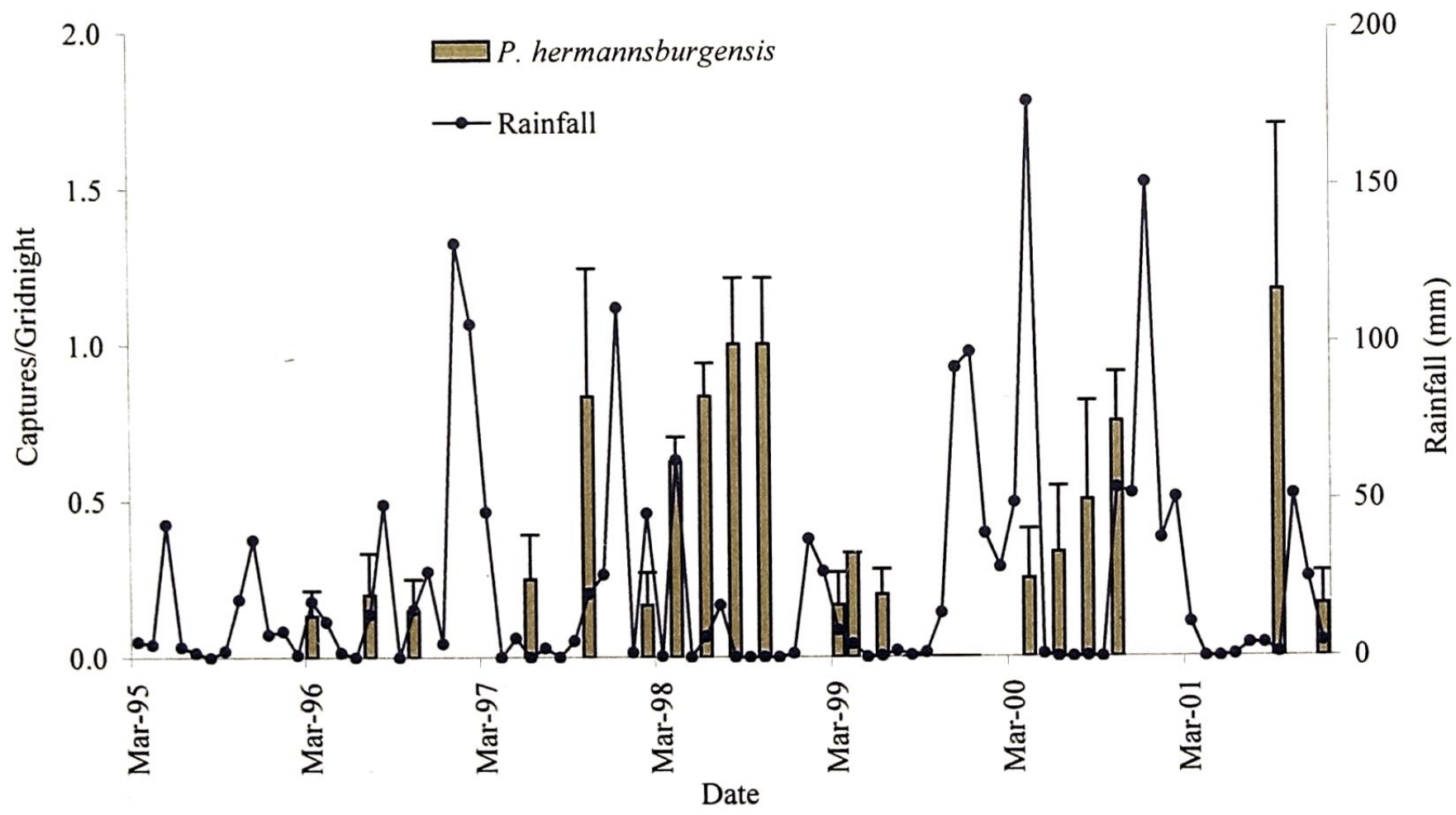
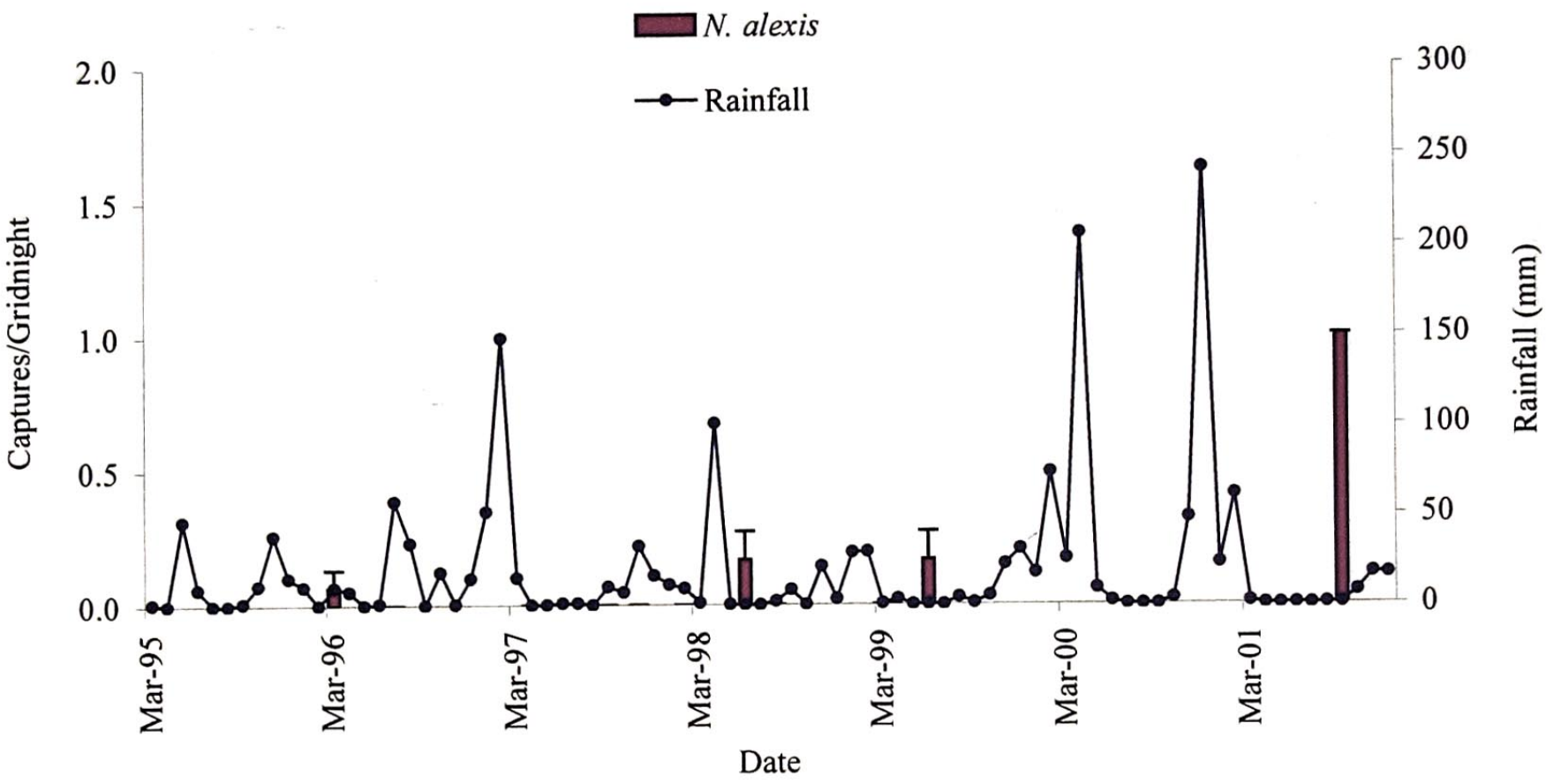


Figure 3.9. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Plum Pudding site. Within-trip recaptures are not included.

a.



b.

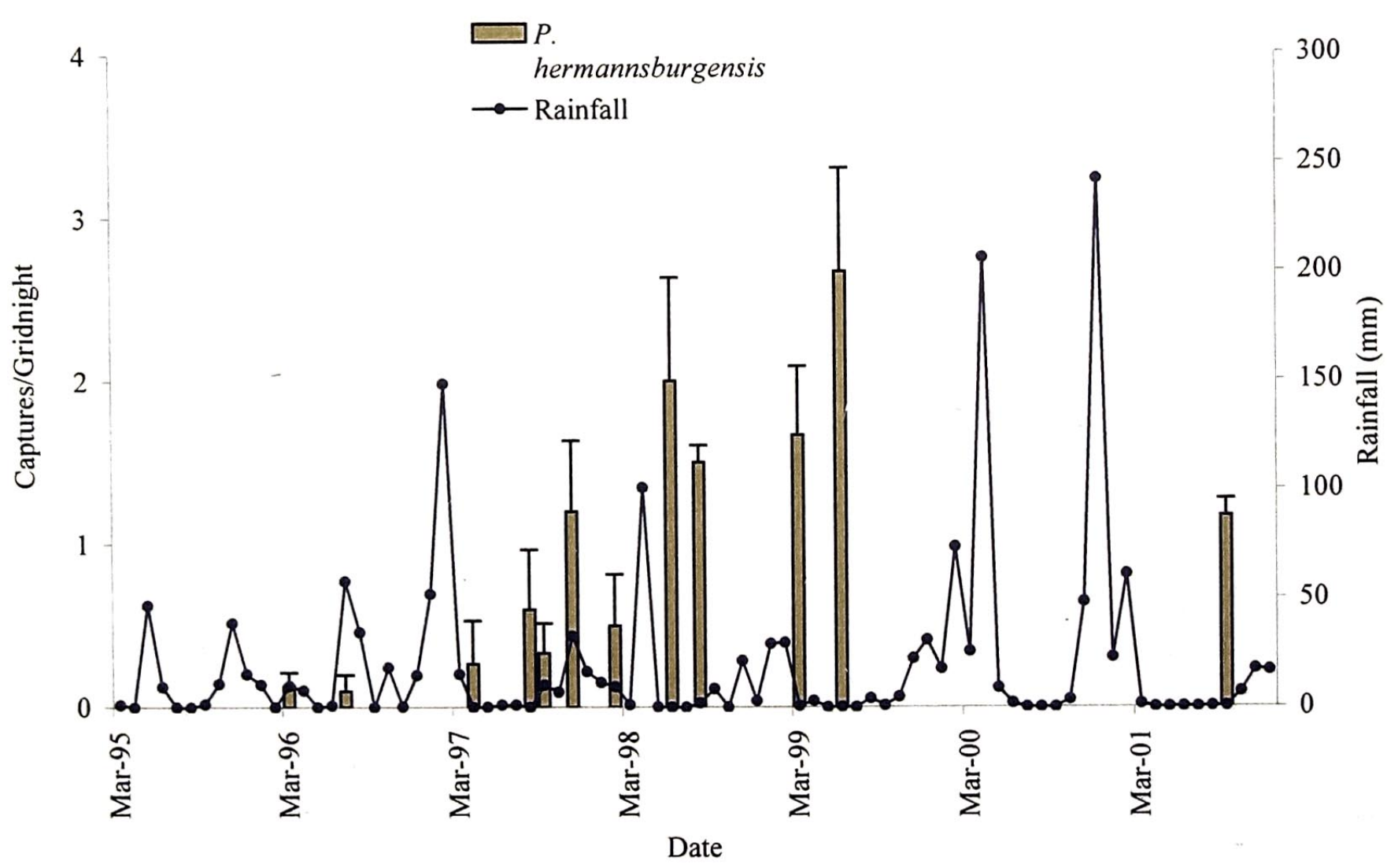
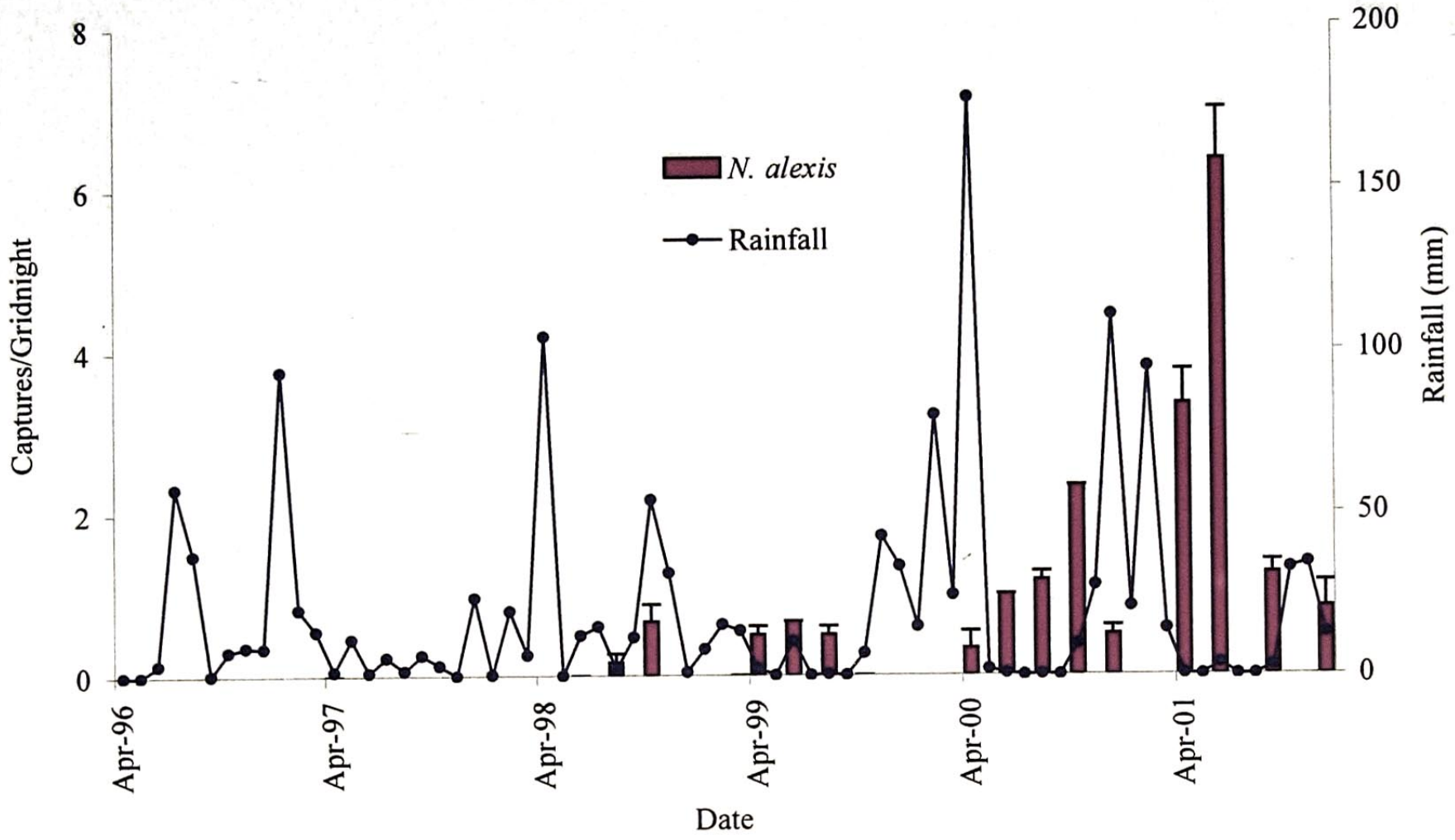


Figure 3.10. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for South site. Within-trip recaptures are not included.

a.



b.

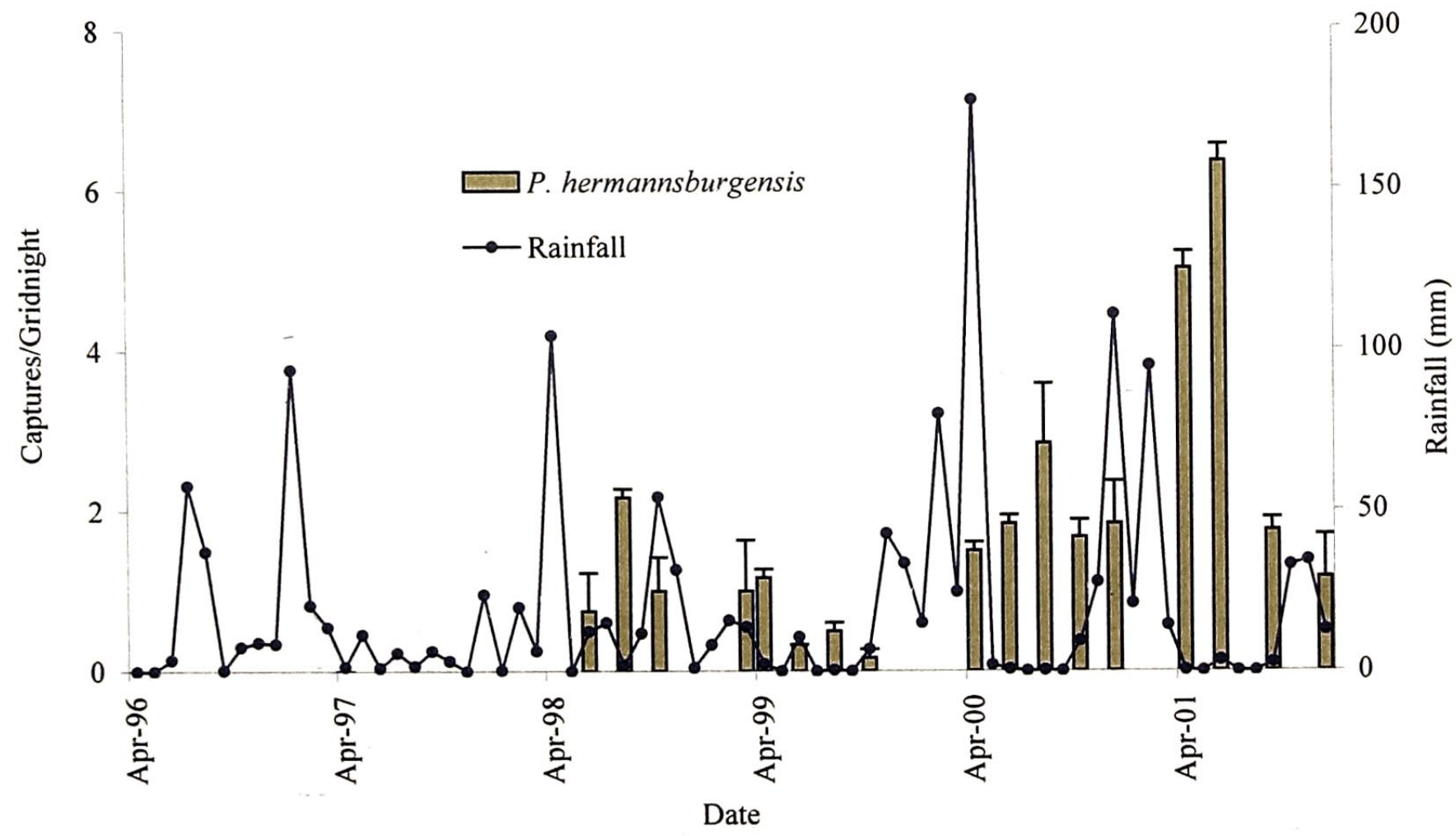
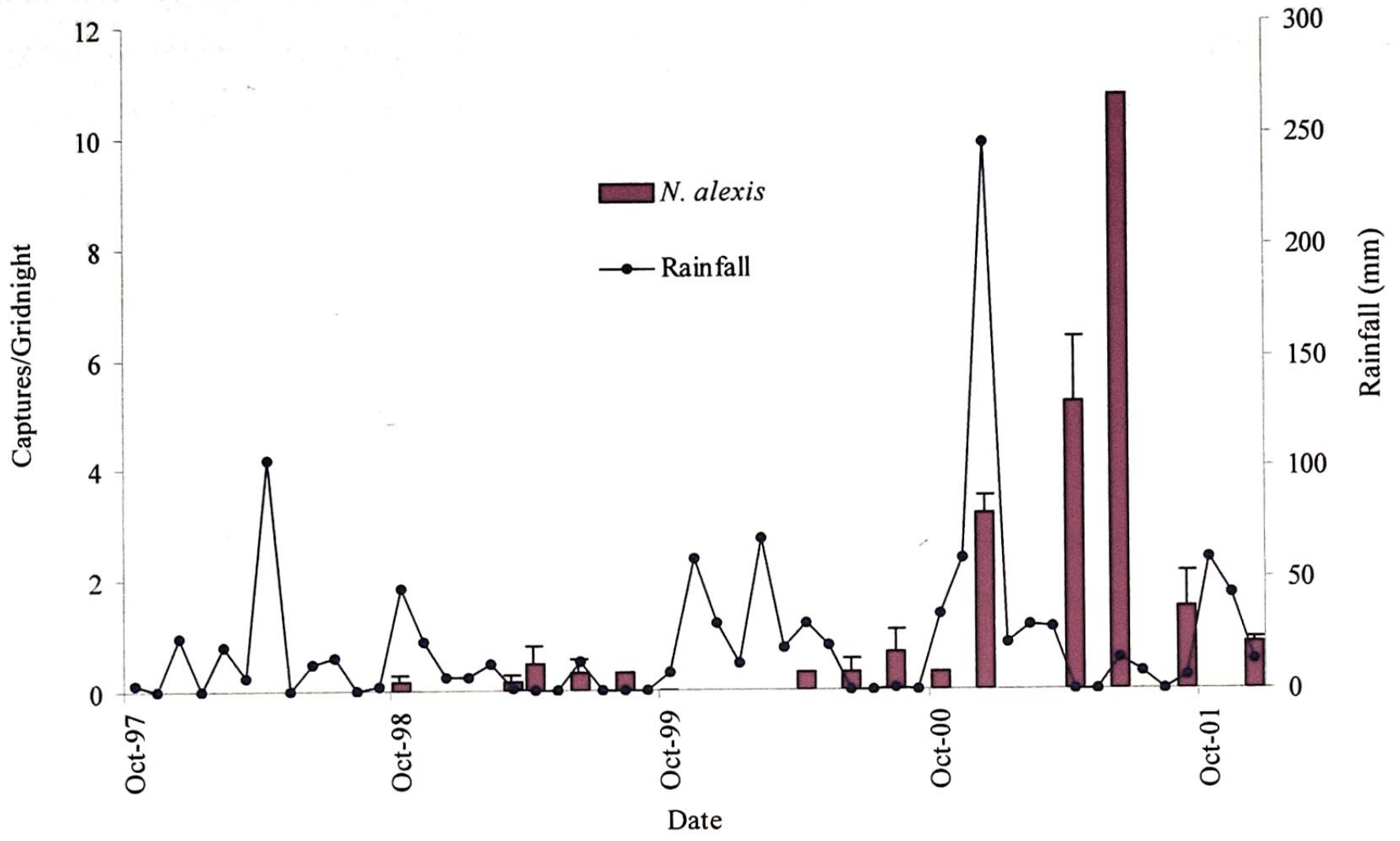


Figure 3.11. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Tobermorey East site. Within-trip recaptures are not included.

a.



b.

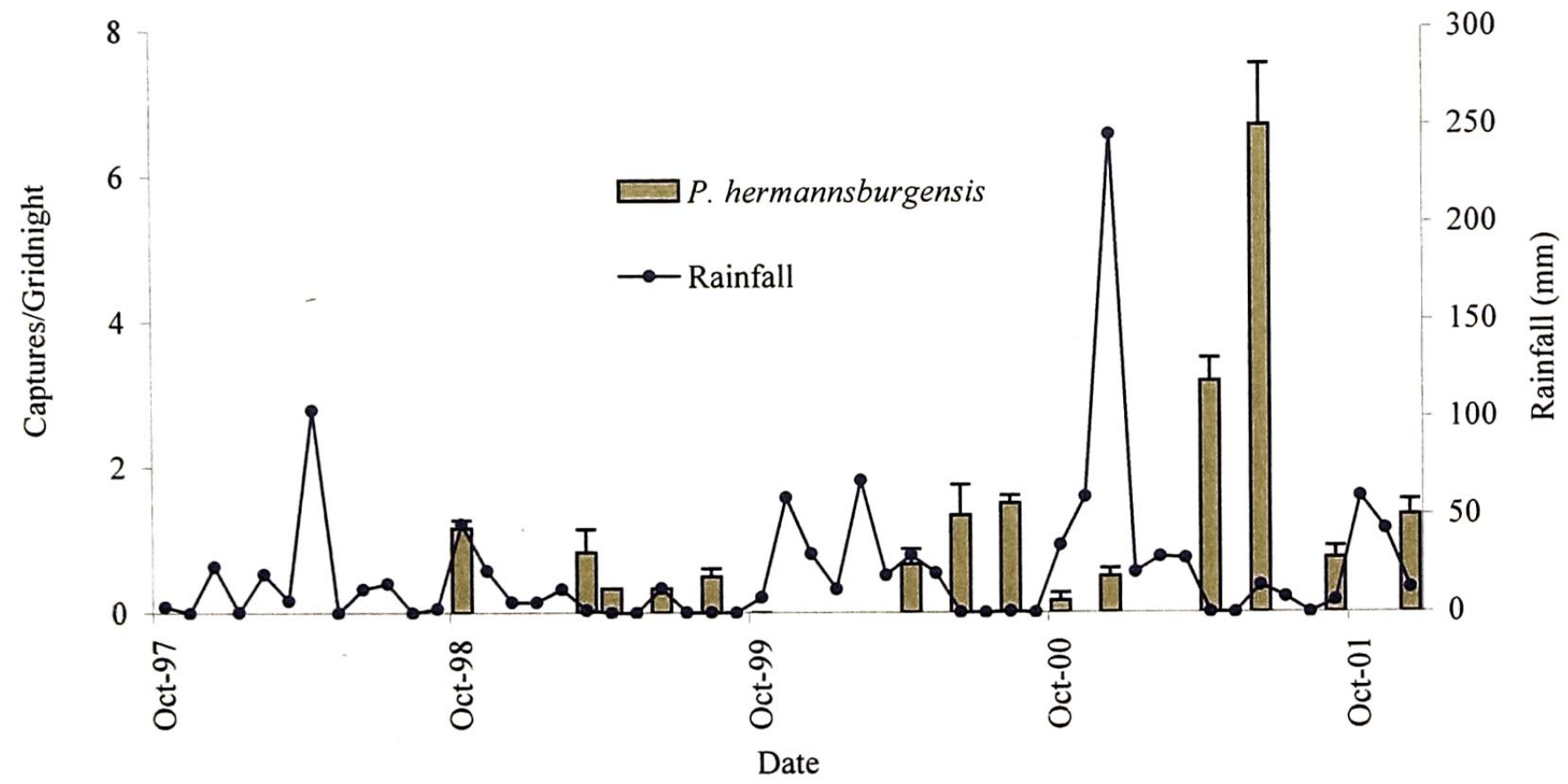


Figure 3.12. Captures per gridnight (+ SE) for *N. alexis* (**a**) and *P. hermannsburgensis* (**b**) plotted with monthly rainfall totals for Tobermorey West site. Within-trip recaptures are not included.

1999, capture rates of the two species began to increase from 2000 to peak during winter 2001 after the 2000 rains. In addition, after the rains of 1997, an increase in abundance of one, or sometimes both species was observed in 1998 at some sites (Carlo, Cravens Peak, Field River South, Plum Pudding). At Naibar and South, *P. hermannsburgensis* showed a stronger response to the 1997 rains than it did to the 2000 ones, with capture rates peaking respectively in October 1998, and June 1998. Moreover, two more peaks for this species occured in March 1999 and June 1999, at South, following no major rainfall event (Figure 3.10).

An important point to observe in comparing capture rates of the two species amongst study sites is the magnitude of their response to rainfall. Capture rates at Ethabuka, Field River South, Koonamuka Swamp West, and Tobermorey West are very high if compared with capture rates at Plum Pudding and South. Furthermore, the capture rates of the two species also differ in the magnitude of their responses to rainfall at Carlo, Ethabuka, Field River North, Field River South, Koonamuka Swamp East, Tobermorey West, and South, with one species being much more abundant than the other. However, there is considerable agreement in the way the two species responded to rainfall at each site, with only South and Naibar sites producing non-significant correlations (Table 3.2).

Tables 3.3 to 3.14 show correlation coefficients (r) for comparisons of monthly capture rates for the two species with rainfall, expressed as the modified CDMR function, at varying time lags for each site. Results suggested a lack of a consistent pattern for all twelve sites, and between the two species. For example at South site weak correlations were observed, with only *N. alexis* responding with a positive, strong correlation ($P<0.05$) to rainfall lagged by nine months. At Ethabuka site many significant correlations were found. Other significant correlations were observed at Carlo, Cravens Peak, Koonamuka Swamp East, Koonamuka Swamp West, Naibar, Plum Pudding, and Tobermorey West sites. No significant results were found at Field River North and South, and Tobermorey East. Generally, correlations were highest 3-6 months after rain, and all significant correlations were positive. These results, when compared with the graphs, show some correspondence with the delays before populations peaked following the highest rainfall events. In addition, it must be considered that correlation coefficients are often very similar between adjacent lag periods, so that differences in lag periods of 1-2 months may be more virtual than real (Dickman *et al*. 1999).

Table 3.3. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05 ***P*<0.01 ****P*<0.001

Ethabuka

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.452**	0.439**
CDMR(exp) (t=1)	0.464**	0.467**
CDMR(exp) (t=2)	0.409*	0.421*
CDMR(exp) (t=3)	0.544***	0.520***
CDMR(exp) (t=4)	0.620***	0.584***
CDMR(exp) (t=5)	0.678***	0.677***
CDMR(exp) (t=6)	0.600***	0.407*
CDMR(exp) (t=7)	0.432*	0.262
CDMR(exp) (t=8)	0.361	0.239
CDMR(exp) (t=9)	0.333	0.241
CDMR(exp) (t=10)	0.407*	0.318
CDMR(exp) (t=11)	0.416*	0.37
CDMR(exp) (t=12)	0.344	0.303

Table 3.4. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05

Carlo

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	-0.140	-0.069
CDMR(exp) (t=1)	0.059	0.238
CDMR(exp) (t=2)	0.062	0.160
CDMR(exp) (t=3)	-0.137	0.212
CDMR(exp) (t=4)	-0.101	0.188
CDMR(exp) (t=5)	0.099	0.152
CDMR(exp) (t=6)	0.245	0.251
CDMR(exp) (t=7)	-0.034	0.046
CDMR(exp) (t=8)	0.095	0.207
CDMR(exp) (t=9)	0.263	0.346
CDMR(exp) (t=10)	0.280	0.285
CDMR(exp) (t=11)	0.499	0.471
CDMR(exp) (t=12)	0.625*	0.522

Table 3.5. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05 ***P*<0.01

Cravens Peak

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.189	0.391
CDMR(exp) (t=1)	0.400	0.477
CDMR(exp) (t=2)	0.454	0.454
CDMR(exp) (t=3)	0.605*	0.583*
CDMR(exp) (t=4)	0.596*	0.575
CDMR(exp) (t=5)	0.662**	0.644**
CDMR(exp) (t=6)	0.687**	0.655**
CDMR(exp) (t=7)	0.591*	0.541
CDMR(exp) (t=8)	0.530	0.522
CDMR(exp) (t=9)	0.506	0.379
CDMR(exp) (t=10)	0.463	0.389
CDMR(exp) (t=11)	0.369	0.386
CDMR(exp) (t=12)	0.376	0.380

Table 3.6. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). ~*P*=0.051

Field River North

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.565	0.496
CDMR(exp) (t=1)	0.535	0.519
CDMR(exp) (t=2)	0.558	0.510
CDMR(exp) (t=3)	0.643	0.617
CDMR(exp) (t=4)	0.188	0.118
CDMR(exp) (t=5)	0.318	0.260
CDMR(exp) (t=6)	0.432	0.397
CDMR(exp) (t=7)	0.504	0.408
CDMR(exp) (t=8)	0.593	0.412
CDMR(exp) (t=9)	0.687~	0.538
CDMR(exp) (t=10)	0.439	0.452
CDMR(exp) (t=11)	0.350	0.349
CDMR(exp) (t=12)	0.037	-0.030

Table 3.7. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995).

Field River South

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	-0.418	-0.270
CDMR(exp) (t=1)	-0.407	-0.225
CDMR(exp) (t=2)	-0.437	-0.267
CDMR(exp) (t=3)	-0.375	-0.292
CDMR(exp) (t=4)	-0.223	-0.167
CDMR(exp) (t=5)	-0.126	-0.166
CDMR(exp) (t=6)	-0.022	-0.049
CDMR(exp) (t=7)	0.096	-0.050
CDMR(exp) (t=8)	0.206	-0.008
CDMR(exp) (t=9)	0.313	0.111
CDMR(exp) (t=10)	0.350	0.223
CDMR(exp) (t=11)	0.413	0.419
CDMR(exp) (t=12)	0.279	0.071

Table 3.8. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). ***$P<0.001$ ~$P=0.051$

Koonamuka Swamp East

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.202	0.418
CDMR(exp) (t=1)	0.320	0.37
CDMR(exp) (t=2)	0.396	0.441
CDMR(exp) (t=3)	0.602	0.552
CDMR(exp) (t=4)	0.662~	0.622
CDMR(exp) (t=5)	0.650	0.519
CDMR(exp) (t=6)	0.819***	0.607
CDMR(exp) (t=7)	0.169	0.134
CDMR(exp) (t=8)	0.159	0.116
CDMR(exp) (t=9)	-0.013	-0.248
CDMR(exp) (t=10)	0.079	-0.088
CDMR(exp) (t=11)	0.167	0.095
CDMR(exp) (t=12)	0.132	0.164

Table 3.9. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05

Koonamuka Swamp West

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.184	0.161
CDMR(exp) (t=1)	0.448	0.516
CDMR(exp) (t=2)	0.511	0.589
CDMR(exp) (t=3)	0.663	0.658
CDMR(exp) (t=4)	0.713*	0.707*
CDMR(exp) (t=5)	0.669	0.485
CDMR(exp) (t=6)	0.686*	0.469
CDMR(exp) (t=7)	0.371	0.136
CDMR(exp) (t=8)	0.303	0.072
CDMR(exp) (t=9)	0.306	0.137
CDMR(exp) (t=10)	0.443	0.399
CDMR(exp) (t=11)	0.594	0.572
CDMR(exp) (t=12)	0.570	0.569

Table 3.10. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05 ***P*<0.01

Naibar

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.283	0.099
CDMR(exp) (t=1)	0.491	0.280
CDMR(exp) (t=2)	0.581	0.320
CDMR(exp) (t=3)	0.742*	0.466
CDMR(exp) (t=4)	0.772**	0.466
CDMR(exp) (t=5)	0.657	0.244
CDMR(exp) (t=6)	0.596	0.347
CDMR(exp) (t=7)	0.090	0.048
CDMR(exp) (t=8)	0.033	0.105
CDMR(exp) (t=9)	0.059	0.099
CDMR(exp) (t=10)	0.316	0.281
CDMR(exp) (t=11)	0.319	0.122
CDMR(exp) (t=12)	0.353	0.066

Table 3.11. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05 ***P*<0.01

Plum Pudding

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.410	0.028
CDMR(exp) (t=1)	0.630	0.21
CDMR(exp) (t=2)	0.654	0.253
CDMR(exp) (t=3)	0.631	0.395
CDMR(exp) (t=4)	0.599	0.445
CDMR(exp) (t=5)	0.684*	0.587
CDMR(exp) (t=6)	0.653	0.713*
CDMR(exp) (t=7)	0.678*	0.708*
CDMR(exp) (t=8)	0.534	0.732**
CDMR(exp) (t=9)	0.470	0.632
CDMR(exp) (t=10)	0.148	0.426
CDMR(exp) (t=11)	-0.016	0.198
CDMR(exp) (t=12)	-0.146	0.057

Table 3.12. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). **P*<0.05

South

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.046	-0.265
CDMR(exp) (t=1)	0.109	-0.126
CDMR(exp) (t=2)	0.062	-0.204
CDMR(exp) (t=3)	0.214	-0.465
CDMR(exp) (t=4)	0.289	-0.245
CDMR(exp) (t=5)	0.433	-0.307
CDMR(exp) (t=6)	0.480	-0.307
CDMR(exp) (t=7)	0.731	-0.188
CDMR(exp) (t=8)	0.816	-0.125
CDMR(exp) (t=9)	0.859*	0.026
CDMR(exp) (t=10)	0.432	-0.088
CDMR(exp) (t=11)	0.079	-0.005
CDMR(exp) (t=12)	0.220	-0.223

Table 3.13. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995).

Tobermorey East

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	-0.004	0.161
CDMR(exp) (t=1)	0.194	0.316
CDMR(exp) (t=2)	0.251	0.364
CDMR(exp) (t=3)	0.489	0.595
CDMR(exp) (t=4)	0.544	0.716
CDMR(exp) (t=5)	0.414	0.326
CDMR(exp) (t=6)	0.462	0.310
CDMR(exp) (t=7)	0.130	0.145
CDMR(exp) (t=8)	0.016	0.111
CDMR(exp) (t=9)	0.200	0.192
CDMR(exp) (t=10)	0.304	0.247
CDMR(exp) (t=11)	0.421	0.400
CDMR(exp) (t=12)	0.493	0.500

Table 3.14. Correlation coefficients for capture rates of the two species of rodents with the modified CDMR with time lags in months (t). *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). *$P<0.05$ ~$P=0.052$

Tobermorey West

Correlation	***N. alexis***	***P. hermannsburgensis***
CDMR(exp) (t=0)	0.413	0.216
CDMR(exp) (t=1)	0.607	0.586
CDMR(exp) (t=2)	0.701	0.737
CDMR(exp) (t=3)	0.767	0.807*
CDMR(exp) (t=4)	0.751	0.774
CDMR(exp) (t=5)	0.772	0.785~
CDMR(exp) (t=6)	0.741	0.752
CDMR(exp) (t=7)	0.290	0.181
CDMR(exp) (t=8)	0.072	-0.041
CDMR(exp) (t=9)	-0.024	-0.101
CDMR(exp) (t=10)	-0.019	-0.094
CDMR(exp) (t=11)	-0.008	-0.009
CDMR(exp) (t=12)	0.078	0.062

3.4. Discussion

3.4.1. Rainfall and rodent population dynamics

The results showed that there was some correspondence between eruptions of the two rodent species, *N. alexis* and *P. hermannsburgensis*, and the occurrence of heavy rainfall. At all sites in winter 2001 a very high density of rodents was recorded, following the extremely wet year of 2000. At Ethabuka two previous eruptions were observed, in mid 1991 and in mid 1992, following exceptional rain events in early 1991 and early 1992. Although rodent populations peaked with different delays from the last rainfall at different sites, the pattern of eruption was similar everywhere, with populations increasing from low densities, then peaking briefly, before declining again within a further six months. Several studies have documented a similar response of these species in arid Australia (Finlayson 1939, Newsome and Corbett 1975, Carstairs 1976, Masters 1993, Predavec and Dickman 1994, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999), and of other rodents in other arid regions of the world (Beatley 1969, Whitford 1976, Fuentes and Campusano 1985, Jimenez *et al.* 1992, Meserve *et al.* 1995, Jaksic *et al.* 1997, Ernest *et al.* 2000).

In contrast to the eruptions of 1991, 1992 and 2001, other periods of high rainfall failed to trigger population eruptions. Thus, heavy rains in January 1995 and February 1997 failed to prompt population increases, the only exception being a small increase in *P. hermannsburgensis* at some sites in late 1997. Such a lack of response to some very wet periods by rodents also has been documented previously in arid and temperate parts of Australia (Newsome and Corbett 1975, Saunders and Giles 1997, Dickman *et al.* 1999). So, do rodent populations respond to rainfall, and if they do why is their response unpredictable?

Rodent response to rainfall is probably not direct but mediated by other factors, and several steps may be involved in the passage from heavy rainfall to rodent eruptions. Rainfall may increase availability of free water that may in turn trigger reproduction. Rainfall may also influence habitat usage by increasing vegetation cover, and thus facilitate rodent increases by providing improved shelter. Another important effect of rainfall is that it increases food availability and accessibility, and this in turn may trigger rodent explosions. These models may explain the observed fluctuations of the two study species, and they will be evaluated more extensively in the next chapter.

The inconsistent response of rodents to rainfall may have several other possible explanations. Firstly, variability could be explained as an artefact of the choice of rainfall statistic, which may not be the most appropriate to describe the dynamics of the causative effects of rainfall. However, this does not appear likely as the modified CDMR has been shown to be the most appropriate statistic for describing highly variable rainfall regimes (Dickman *et al.* 1999, Mahon 1999), and the exponential modification was constructed using field observations from Ethabuka (Predavec 1994a). More likely is that rainfall does not directly control increases in rodent abundance, and that magnitude of the response does not necessarily reflect the amount of rain. At Ethabuka, for example, the increase in rodent abundance in winter 1992, following the rains of February 1992, was very similar to that following the rains of 1991, and much bigger than the response to the February 1997 rains, even though the amount of rainfall in early 1992 was less than on the other two occasions. At Carlo, heavy rain in early 1995 did not produce the same effect as a smaller rainfall in April 1998 that triggered an increase of similar magnitude to that produced by the very high rainfall of April 2000. Similarly inconsistent patterns of response were observed at Cravens Peak, Naibar, and other sites. At Plum Pudding and South, *P. hermannsburgensis* peaked in abundance after moderate rains in December 1997, April 1998, and March 1999, but not after the heavy rains of April 2000 and December 2000. Perhaps this species is better able to exploit small increases in resources than *N. alexis*, and its eruptions can be amplified in periods of reduced competition (Dickman *et al.* 1999).

Apart from water, soil nutrients are an important factor limiting primary productivity. Australian desert soils are very poor, with low concentrations of nitrogen and phosphorus (Stafford Smith and Morton 1990, Latz 1996). The majority of nutrients are generally present in the top 5-10 cm of the soil in arid Australia (Charley and Cowling 1968, West 1981, Stafford Smith and Morton 1990), and they are therefore subject to movement by water and wind erosion (Noy-Meir 1981). Consequently soil depletion is likely to occur, especially after rain has induced flushes of vegetation growth. Thus, subsequent rain may not stimulate a marked response from vegetation until nutrients have been returned to the soil, resulting in less abundant seeding, and a minimal increase in food availability for rodents (Morton and Baynes 1985, Stafford Smith and Morton 1990).

This scenario could explain the lack of rodent response to the heavy rains of 1995 in the study area. The rains of 1991 and 1992, producing an explosion in primary productivity, likely left the soil completely deprived of nutrients, and so incapable of providing resources for a long period of time. Seed production seemed substantially less in

1995 than after the 1991 and 1992 rains (C.R. Dickman *pers. comm.*). Dissimilar responses to the rains of 1997 and 1998 at different sites may be interpreted again as resulting from differential availability of soil nutrients across the study area, which differs subtly in soil types, grid positions and on-site rainfall. Several models of rodent eruptions in Australia have proposed that extended dry periods followed by heavy rains are ideal conditions for an outbreak (Saunders and Giles 1977, Southgate and Masters 1996, Pech *et al.* 1999). Eruptions at all sites in winter 2000 and 2001 fit these models in that a long period of soil enrichment (nearly ten years) was necessary before high nutrient levels were re-established and vegetation could take full advantage of heavy rains in April and December 2000. Nevertheless, an increase in primary productivity was evident after the 1995 and 1997 rains, and other granivorous animals, such as budgerigars and chats, took advantage of this situation (P.S. Mahon *pers. comm.*), increasing considerably in numbers. Perhaps the amount of seed was not sufficient to trigger an increase in rodent populations, or other factors prevented rodent population eruptions in these years.

Sometimes populations achieve very low densities that would minimise or delay the response to rainfall. In fact, at low densities the absolute increase in abundance, assuming an exponential rate of increase, will be much less for a given period of time. At very low densitites, the *Allee effect* (Emlen 1984) further predicts difficulties of individuals finding mates for reproduction. At this stage recruitment becomes vital for the survival of the population, and it can initiate increases in otherwise not dynamic populations (see above). Variations in responses to rainy events in different areas could then be attributed to differences in the intial density of the population (Dickman *et al.* 1999), and perhaps also to its demographic structure (sex ratio, number of juveniles).

Competition with other taxa is another potentially important force in determining rodent population dynamics. Although omnivores, Australian desert rodents have a large portion of their diet represented by seeds and green plant material (Murray *et al.* 1999). This could lead to competition with other herbivorous and granivorous taxa, such as birds and ants, which are more specialised and better harvesters than rodents (Tischler 1998), especially during drought when primary productivity is low. Similar overlaps may occur at times with invertebrate resources (Morton 1985, Predavec 1994a, 1997a, Reid 1995), especially with specialist insectivores such as dasyurids (Fisher and Dickman 1993). Thus, limited rain-induced resources are likely to be depleted by more specialist and more quickly increasing taxa than rodents before a substantial increase in rodent density is observed (Brown and Davidson 1977, Brown *et al.* 1979a).

Predation is another extrinsic factor that contributes to shaping rodent population dynamics. Predation can suppress rodent outbreaks, particularly if previous increases in rodent abundance have stimulated increases in the numbers of predators (Newsome and Corbett 1975, Lima *et al.* 2002). It can also accelerate declines and maintain population densities at very low levels, thus preventing further increases. Limited evidence suggests that red foxes *Vulpes vulpes* and feral cats *Felis catus* may have suppressed rodent populations during the period 1995-1997 (Mahon 1999).

Several models have been suggested to interpret rodent eruption phenomena (Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999, Krebs 1999). Pech *et al.* (1999) presented a review of the available models for predicting plagues in Australia, using the house mouse (*Mus domesticus*) as an example. Different-scale models were proposed (broad-scale, district and small-scale, and process models) that can be applied with some modifications to eruptions of native rodents in arid Australia. The review showed clearly that there are a number of common features likely to initiate and control an increase in rodent abundance: a plague trigger (a correct sequence of wet and dry periods) that enhances primary productivity and thus facilitates high reproduction and dispersal, and an increase in refuge accessibility. Predation and disease, two density-dependent factors, were considered as being modifiers of rodent population dynamics (Pech *et al.* 1999, Begon 2003). Several models suggest also that landscape heterogeneity likely interacts with regulatory processes, providing a potential explanation for the variability in response observed by rodents amongst different sites in the present study. That is, different habitat types, floristic communities, rainfall and microclimates between sites will lead to temporal asynchrony in the food supply, and in refuge accessibility. This could have been the case in the study area where different study sites may present marked differences along rain and fire gradients. Krebs *et al.* (1995b) and Krebs (2003) proposed further that intrinsic regulatory processes shape rodent population dynamics, with social organisation and behaviour filtering the response of mice to extrinsic factors. Because of the difficulties of testing this hypothesis in nature, however, it is easier, at least initially, to analyse the extrinsic causes and mechanisms driving rodent population dynamics.

3.4.2. How do populations respond to rainfall?

Mechanisms of population increase include enhanced reproduction, survival and/or immigration rates. In arid Australia, many studies have documented that reproduction is

the main factor facilitating increases of rodent populations (Finlayson 1940, 1941, Plomley 1972, Masters 1993, Predavec 1994b, Southgate and Masters 1996, Dickman *et al.* 1999). Higher numbers of reproductively active females have been observed in populations during periods of increase after rainfall, but at population peaks the proportion of reproductive females declines (Finlayson 1940, 1941, Reid *et al.* 1993, Predavec 1994b, Southgate and Masters 1996). In North America Van der Graff and Balda (1973) found similarly that kangaroo rats (*Dipodomys merriami*) had higher reproductive rates at one site that received high rainfall over the preceding 12 months than at a second site where rainfall had been low. Aseasonal and opportunistic breeding has been observed in Australian arid-zone rodents (Happold 1976, Breed 1979, 1990a), but reproduction is not always associated strongly with rainfall. Breed (1979, 1990a) reported that reproduction can still occur in some species in dry periods. Mahon (1999) found no difference in the proportion of adult females reproductively active between years of above and below-average rainfall. Changes in reproductive activity did not appear to be driven by rainfall, but instead were associated with density, with reproductive rates being high when population numbers were low, and declining at peak densities. Such findings are consistent with inverse density dependent reproduction during eruptions of the study species, as observed by Predavec (1994a, 1994b) and Southgate and Masters (1996). Breed (1979) proposed a similar explanation as a response to high densities. However, the reproductive synchrony within and between species found by Reid *et al.* (1993) and Predavec (1994a) suggests that rodents do show some response to external cues (Stenseth and Ims 1993, Korpimäki and Krebs 1996, Wolff 2003), rather than being controlled exclusively by intrinsic mechanisms (Krebs 2003). Considering the high energetic demands of reproduction (Sadleir 1969), the most likely external cue must be food availability. Several studies have shown that food availability controls the timing of reproduction generally in rodent species (Kemper 1980, Breed 1990a, Boutin 1990, Fox *et al.* 1993, Predavec 2000). Even during dry periods, localised or aseasonal rains can trigger some reproduction and facilitate increases in populations.

Immigration is an alternative mechanism of population increase. Dickman *et al.* (1995) have shown that long-range movements occur independently of sex, age and reproductive status in desert-dwelling small mammals, but tend to increase during and after rain. In addition, animals move towards areas of rainfall to exploit rain-induced resources. It is likely that the two study species move opportunistically to escape from drought-affected areas with diminished resources to resource-rich sites. However, from the results of this chapter and from previous studies (Newsome and Corbett 1975), it is clear that eruptions

of these species can occur simultaneously over vast areas of arid Australia. Thus, it is unlikely that immigration is a major force in shaping rodent population dynamics. Nevertheless, some peculiar results of this chapter (isolated peaks in capture rates in 1998 and 1999 at South, in 1998 at Plum Pudding, and in 1998 at Naibar) can be interpreted as due to immigration of rodents from close, less resource-rich areas (see Predavec 2000). Recruitment of new individuals from neighbouring areas can speed population increases that would be otherwise impossible because of the very low density of the *in situ* population. However, the recruitment process may be complex, and dependent on the social structure of the host population (Krebs 2003). Some models take account of density-dependent mechanisms of recruitment (Danielson and Stenseth 1992, Krebs 2003), but have been little applied.

Another possible factor involved in rodent eruptions is the survival rate of juveniles. If individual survival is limited by food (Boutin 1990), rain-induced flushes in resources may lead to eruptions by increasing the survival rate of juveniles, rather than increasing the reproductive rate of the population. Mahon (1999) found that the proportion of juveniles versus adults increased after rainfall. The results of Meserve *et al.* (1995) confirmed that rain increased the survival rates of four desert rodent species in northcentral Chile during eruptions. In contrast, reproduction in these species showed only small increases.

Thus it is possible that, following rains, all the previous mechanisms act together with different intensities and at different times to start population eruptions in desert rodents.

3.4.3. Why do populations respond to rainfall?

Despite limited concordance in population fluctuations between sites, there was stronger synchrony in the timing and duration of eruptions of the two study species within sites. This suggests that the species' populations respond to similar extrinsic factors. At the same time, the results also suggested that rodents do not respond directly to rainfall. In desert environments rainfall can dramatically augment primary productivity. Establishment of perennials (Kemp 1983, Bowers 1996), increased cover, diversity, and seed production in annuals (Loria and Noy-Meir 1979, Gutiérrez *et al.* 1993) are all rain-induced effects on vegetation. Such changes in vegetation composition, production and structure are likely to create a suitable environment for rodent eruptions. If rodent populations are often limited by food (Newsome 1970, Boutin 1990, Predavec 2000), then new rain-induced resources should stimulate their increase. In arid regions outside Australia, several studies have

reported population increases in desert rodents after rain, linked to strong increases in annual herbs and grasses, and seeds (Beatley 1969, Pefaur *et al.* 1979, Jaksic *et al.* 1997).

A critical question is whether rodent eruptions are triggered by the quantity or by the quality of food that becomes available after heavy rains. Some studies in North America have suggested that nutrients are more important than the quantity of food in limiting reproduction and survival in rodents (Hoffman 1958, Batzli and Pitelka 1971, Cole and Batzli 1978). Nitrogen in the form of proteins can be a critical limiting factor in reproduction and juvenile survival (White 1978, 1993, 2002, Bomford and Redhead 1987), while energy in the form of carbohydrates may not be in short supply (Stafford Smith and Morton 1990, White 1993). Thus it is possible that increased availability of nutrients facilitates eruptions of rodents in arid Australia (Morton and Baynes 1985, Stafford Smith and Morton 1990).

Studies in North America show that reproductive timing in rodents often coincides with the presence of green vegetation in the environment (Chew and Butterworth 1964, Beatley 1969, Batzli and Pitelka 1971), and in the diet of rodents (Batzli and Pitelka 1971, Bradley and Maurer 1971). Breeding out of season in voles can be induced by addition of green grass to their diet (Negus and Berger 1977). These effects might be generated by chemical triggers other than water in green vegetation (Reynolds 1954, Chew and Butterworth 1964, Allen and Hume 1997), but increased availability of water still seems to be important. The fact that abundance of *N. alexis* was not correlated with seed availability may suggest that this species is more dependent on water availability, in the form of green vegetation (Predavec 1994a). This is a large and complex topic; subsequent chapters of this thesis will deal more completely with the water content and other constituents of food, and their role in rodent diet selection.

3.4.4. Why do rodent populations decline?

The results of this chapter showed that rodent populations decline rapidly within six months from their eruption peaks. The immediate cause of this may be the depletion of food following the heavy exploitation of resources when populations are at high density. Studies in North America and Australia have reported that granivores can impoverish the seed bank and abundance of desert annuals over time (e.g. Brown and Davidson 1977, Brown *et al.* 1979b, Inouye *et al.* 1980, Predavec 1994a, 1997a). Moreover, when water becomes scarce, vegetation growth stops, annuals and other green vegetation disappear,

plant cover and diversity decline, and in general primary productivity decreases. At Ethabuka, the seed bank declined steeply in 1993, within a year of heavy rainfall (Predavec 1994a), and vegetation structure changed after the rainfall peaks in 1991 and 1992 (C.R. Dickman *pers. comm.*). Dickman *et al.* (1999) estimated a rate of decline of rain-induced seed resources of 20% per month for the current study area. Decline in food availability, and the general impoverishment of the habitat, will eventually cause a decline in food-limited rodent populations, if further rainfall does not follow. Reproduction declined at peak densities or soon after in both 1991 and 1992 for both species (Mahon 1999), perhaps from resource depletion or social suppression of reproductive activity at high population density (Breed 1979, Krebs 2003). Density dependent mechanisms such as suppression of reproduction, diseases (Carstairs 1974, Munger *et al.* 1983, Begon 2003), or cannibalism of young (S Ricci *pers. obs.*, Krebs 2003), can be other factors involved in population decline. In fact, sometimes addition of food cannot prevent population declines (e.g. Krebs and Delong 1965, Cole and Batzli 1978, Taitt *et al.* 1981, Krebs *et al.* 1986, Henttonen *et al.* 1987, Krebs *et al.* 1995a), suggesting that food is not always the main factor in driving declines (Boutin 1990). In 1992 and 1993, Predavec (2000) could not stop population declines of the two study species at Ethabuka, despite adding food to some grids. No evidence of disease was observed during periods of decrease in numbers of the two species at the study area (Dickman *et al.* 1999), but at peak population size the mean mass of adult males of the two species was at its lowest (Predavec 1994a); this suggests that density-dependent mechanisms can play an important role in controlling rodent population dynamics. Finally, predation also may drive population declines. Dramatic increases of terrestrial predators such as feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) often follow rodent eruptions in arid Australia (Newsome and Corbett 1975). It is likely that the intensity of predation differed over the period of study at each site. In fact, at Ethabuka in early 1991, feral cats increased in abundance and red foxes arrived at the site for the first time (Dickman 1996a, Dickman *et al.* 1999), following the heavy rain. These two predators preyed heavily on the two study species in late 1992, when their main prey, the long-haired rat (*Rattus villosissimus*), disappeared from the study area (Predavec and Dickman 1994, Dickman 1996b). Although the two predators themselves declined in 1993, predation pressure on *N. alexis* and *P. hermannsburgensis* may have continued, suppressing increases of the low density populations of the two species despite the significant rainy events of the summers of 1994/95 and 1996/97 (Dickman *et al.* 1999, Mahon 1999).

3.5. Conclusions

The responses of the two study species to rainfall were spatially and temporally variable, with rainfall triggering rodent eruptions on some occasions only. Over the study periods three main eruptive events were observed (in the winters of 1991, 1992 and 2001), although heavy rains were also recorded in the summers 1994/95, 1996/97, April 1998, and April 2000. Responses were differently time-lagged, depending on the study site, although patterns of response by the two species were generally similar within sites. The causes of such variability are not clear. Rain-induced increases in food resources seem to be particularly important in driving the dynamics of food-limited rodent populations. However, it remains to be explained if is the quantity or the quality of food that has the strongest effect on rodent numbers. Moreover, rain-induced increases in availability of free water and vegetation cover may also be crucial in driving rodent eruptions.

In the next chapter I examine rodent population dynamics in the light of these models and their implications for rodent diets and foraging strategies.

CHAPTER 4: DIET, FOOD RESOURCES AND RAINFALL

4.1. Introduction

4.1.1. Models and hypotheses

The pattern analyses presented in Chapter 3 showed a variable response of Simpson Desert rodent populations to rainfall, with strong responses to rainfall being evident at times but no apparent responses detected at others. A possible explanation for these results is that rodents do not respond directly to rainfall events, but to the primary productivity governed by them. Strong fluctuations in resources are common in desert ecosystems and result from the extreme unpredictability of climate (Kemp 1989). Levels of resource distribution and abundance are limited mainly by water availability (Kemp 1989, Inouye 1991, Polis 1991), and interactions between consumers and their resources are affected directly by such limitation (Noy-Meir 1973, Reichman 1975). The next step in understanding the fluctuations of desert rodent numbers is to interpret them in the light of resource availability, and more precisely food availability.

Three models might explain the patterns observed in chapter 3:

1) *Rainfall increases availability of free water*. This may allow an increase in lactation and therefore an increase in reproduction. Animals would also be released from the pressure of feeding on food rich in metabolic water but lacking in nutrients (carbohydrate-rich food). However, free water from rainfall is available for only a short period in claypans (about two months, C. R. Dickman *pers. comm.*), and rodent eruptions generally last longer than this. Consequently, free water is unlikely to be the only factor that starts and sustains rodent population increases and peaks. Moreover, nights with dew provide free water for 3-4 months of the year, but rodents do not respond to this (C. R. Dickman *pers. comm.*). In addition, desert rodents show diverse adaptations to water scarcity and thus may not be strongly limited by its absence. Hence, this model can be rejected.

2) *Rainfall increases vegetation cover*. Vegetation cover may allow rodents to escape predation, to exploit a greater range of microhabitats, and improve burrowing conditions due to the ameliorating effect of plant roots in the ground. If this model is true, we would expect three predictions to be satisfied. Firstly, vegetation cover should be correlated with rainfall, with likely lags of several days to weeks being observed. Secondly, rodent capture rates should be correlated with vegetation cover. Thirdly, any changes in rodent diet should

be independent of changes in plant cover. Unfortunately, there are insufficient data as yet to be able to evaluate this model, at least for the study area.

3) *Rainfall increases food availability and accessibility*. Rainfall triggers primary productivity, softens the soil, allowing easier exploitation of seed banks (Johnson and Jorgensen 1981, Vander Wall 1993), and may increase secondary productivity also (e.g. invertebrate abundance) (Fisher and Dickman 1993). The increase in food availability may trigger reproduction (Newsome and Corbett 1975, Masters 1993, Predavec and Dickman 1994, Dickman *et al.* 1999), immigration (Newsome and Corbett 1975, Stafford Smith and Morton 1990, Predavec 2000), enhance juvenile survival, loosen intra- and inter-specific competition pressure, and improve the general body condition of individual rodents. If this model is true, we should expect several predictions to be satisfied. Firstly, rainfall should be correlated with food availability (e.g. flowers and seeds should be produced after rain, or be present in the seed bank, and green plant cover should increase). Secondly, rodent capture rates should be correlated with food resources (e.g. seeds on plants or in the seed bank, and green plant cover). Availability and accessibility of food resources should be the primary factors controlling rodent population fluctuations. Thirdly, rodent diet should change with changes in food resources. Diet should reflect resource availability. Finally, animals will show stronger dietary selectivity when food resources are more abundant (Pulliam 1974). The third and final predictions distinguish this model most clearly from the vegetation cover model.

The general objective of this chapter is to test the predictions derived from the habitat cover and productivity models, and hence evaluate which model is best able to explain the observed fluctuations of the two species of study rodents. Before this, I first consider the concepts of food availability and exploitation that are inherent in Model 3.

Certain food groups or plant species may occur in different amounts in the diet during rodent increases, peaks, declines and troughs. Moreover, differences in foraging behaviour and selectivity for food may be detected during different phases of the rodent population cycle. This may explain differential use of resources and also contribute to rodent fluctuations. In order to examine these possibilities, in this chapter I divide the cycle of rodent population dynamics into four phases (High, Decreasing, Low, and Increasing), and investigate diet and food availability in each.

Because Chapter 3 showed strong correlations between the capture rates of the two rodent species, we might expect them to respond in similar ways to the models proposed. However, *N. alexis* virtually disappeared for long periods of time from most of the study

sites, while *P. hermannsburgensis* persisted, albeit in small numbers (Dickman *et al.* 1999). For this reason, some dietary differences are expected to occur between the two species.

4.1.2. Food availability

Wiens (1984) stated that resource limitation occurs when any resource is present in a lesser or equal amount relative to the demand of the consumer population. Food limitation can play a major role in population dynamics (Andrewartha and Birch 1954, Lack 1954), especially in depressing population numbers. 'Food abundance' is the quantity of resources present in the ecosystem, independent of the consumers (Johnson 1980, Wiens 1984). 'Food availability' is how consumers perceive the food, and refers to the direct accessibility of the food to consumers (Johnson 1980, Wiens 1984). Both concepts are very difficult to quantify in natural systems, and hence measurements provide only estimates of the true abundance and availability of food resources to consumers. Even the relationship between abundance and availability is often opaque, and the two concepts are mediated by the further concept of accessibility. Not all the food resources present in the system (abundance) will be accessible to the consumers (availability). Moreover, consumers can actively choose to select from a subset of available food resources (selection), further narrowing the variety in their diet (Fisher and Dickman 1993).

Two studies (Murray and Dickman 1994a, b) have shown that the two study species consume three broad categories of food (seeds, plant material and invertebrates), although seeds predominate.

4.1.2.1. Seed availability

Many plant species survive drought by spending a large proportion of their lifecycle in a dormant stage as seeds (Mott and McComb 1974, Inouye *et al.* 1980, Kemp 1989). This is particularly obvious in annual plant species, which constitute up to 40% of the flora in arid regions and whose seeds may remain viable in the soil for many years (Westoby 1980, Kemp 1989, Inouye 1991, Rundel and Gibson 1996). Only when particular combinations of temperature, rainfall and photoperiod are present can germination, rapid growth and seed production occur (Inouye 1991). Thus, it is not only the amount of precipitation that triggers primary productivity but a complex of several factors. This may explain why it is difficult to detect a linear response of rodents to the amount of rainfall.

4.1.2.2. Seed banks

Seeds in the soil and litter comprise the soil seed bank. Several studies on the soil seed bank have been conducted, especially in the northern hemisphere (e.g. Nelson and Chew 1977, Reichman 1984, Inouye 1991, Boeken *et al.* 1995, Pake and Venable 1996, Price and Joyner 1997, Guo *et al.* 1998), and show that it varies greatly both in space (horizontal and vertical dispersion) (Price and Joyner 1997) and in time (transient if seeds germinate shortly after dispersion or persistent if seeds remain in the soil for longer than one year) (Roberts 1981, Reichman 1984, Thompson 1987, Simpson 1989). Despite their spatially and temporally patchy distribution, seed densities in desert soils are often very high. Nelson and Chew (1977) and Price and Joyner (1997) estimated densities of over 100,000 seeds/m^2 in the Mojave Desert of North America. In western New South Wales, Morton (1979) calculated a density of 30,000 seeds/m^2. A lower density of 3,600 seeds/m^2 was found in the Great Basin Desert of North America (Parmenter and MacMahon 1983). In desert soil, the majority of seeds (80-90%) is distributed in the top 2 cm of soil (Childs and Goodall 1973, Reichman 1975, Young and Evans 1975).

4.1.2.3. Seed predation

After dispersal, seeds can germinate, fall into deeper soil levels and be stored in the soil profile, become senescent or be preyed upon by granivorous and omnivorous animals (Kemp 1989, Price and Joyner 1997, Gou *et al.* 1998). Seeds represent a nutritious food source for animals (Golley 1961, Lockard and Lockard 1971, Brown *et al.* 1979b, Reichman 1979, Davidson *et al.* 1980, Inouye *et al.* 1980), being rich in fat, carbohydrates, nutrients and water (Reichman 1977, Kerley & Erasmus 1991). Moreover, they are often easy to find and store.

The two studied rodent species are not strictly granivorous, but seeds do constitute a major component of their diet (Watts 1970, 1977, Murray and Dickman 1994a, b). The soil seed bank can be depleted at a rate of 20% a month through predation (Predavec 1994b), thus rapidly depriving the two rodent species of one of their main food resources. In these circumstances, we might assume that the two rodent species could rapidly become food limited (Predavec 1994a) and responsive to the provision of fresh seed (Predavec 2000).

4.1.3. Food availability and usage

In order to understand intra- and interspecific foraging strategies of animals, a comparison of their diets with available food resources can be employed. In this comparison we must take into account the limitations, biases and constraints of the different methods of diet analysis, estimation of food availability, and food selection (e.g. Smith and Shanduk 1979, Holechek *et al.* 1982, Lechowicz 1982, McInnis *et al.* 1983, Putman 1984, Dickman and Huang 1988, Norbury 1988a,b, Loggers 1991, Norbury and Sanson 1992, Hughes 1993, Campos 1997). Animals are expected to be generalists when food resources are limited and specialists when food availability increases (Pulliam 1974). Moreover, smaller animals should select more nutritious foods than larger animals (e.g. Jarman 1974, Illius and Gordon 1993). In reality, the perception of and the accessibility to food by animals may change drastically over time and space, being controlled and influenced by many biotic and abiotic factors such as physiology, morphology, age, behaviour, social organisation, learning processes, interactions with other organisms (predation, competition, parasitism) (Thompson 1982, Kotler 1984, Hughes 1993), temperature, wind, topography, soil texture and rainfall (Nelson and Chew 1977, Price and Reichman 1987, Randall 1993, Predavec 1994b, McIntyre 2001).

In this study, the focus of diet analysis and estimation of food availability is mainly on seeds, since they represent the major portion of the diet of the two species (Murray and Dickman 1994a). As illustrated above, seeds are patchily present in the environment and show strong spatial and temporal variation. Nevertheless, they constitute a more predictable and stable food resource than other food items such as green plant material and invertebrates (Brown 1973, Reichman 1975), and represent an important reservoir in unpredictable desert environments.

4.1.4. Aims

We need to understand what animals eat at different stages of their population cycle and to consider how they may change their foraging strategies and diet according to food availability. In order to clarify these questions, in this chapter I investigate 1) correlations between rainfall, plant primary production (species abundance, species richness, flowering and seeding) and seed abundance and diversity in the seed bank, 2) the correlation between primary productivity and rodent capture rates, and 3) the diets of the two species during

periods of low, high, increasing and decreasing animal density. In order to clarify the trophic strategy of the two species during these four periods, dietary analyses are compared with plant and seed species availability. These investigations and analyses should allow tests of the three models, above, to be carried out.

All investigations in this chapter were carried out at the Ethabuka site, described in chapters 2 and 3. Data for this site were available from March 1990 to December 2001.

4.2. Materials and Methods

4.2.1. Food availability from plant surveys

In order to index primary production in the study area, plant survey records were examined over a period of twelve years from March 1990 to December 2001. Most of the plant survey data were recorded contemporaneously with trapping data, and on the same grids used to assess rodent population dynamics. For the plant surveys, cover, presence of seeds and flowers were scored for each species present in a 250 cm by 250 cm square around traps 1, 8, 16, 22, 27 and 36 in each of the twelve grids at the study site. The cover of each single species was estimated by eye and expressed as a percentage. Seeding and flowering were expressed as indices of seed/flower presence with scores from 0 to 5 to indicate abundance, from absent (0) to very high abundance (5). Plant species were identified using a reference collection of plant, seed and flower material created from specimens collected in the study area. To provide a further indication of food availability for the rodents, monthly indices of the above-ground seed and flower crops were estimated as follows:

$\text{Index} = \sum_{\text{all species}}$ (mean % cover of seed/flower-bearing plants X mean seed/flower index for seed/flower-bearing plants)

Results were expressed as monthly and total percentages, and plotted graphically, with plant species classified according to family, plant type and period of survival (annual and perennial) for gross analyses. Cover was estimated with and without spinifex (*Triodia basedowii*) since this species dominated both monthly and annually, thus masking the contribution of other plant species and their pattern of cover.

The period of data collection was again divided into four phases following the procedure described above. Because the two rodent species showed slightly different fluctuations in abundance over the study period, the four phases coincided with different patterns of plant cover depending on which rodent species was examined. For this reason analyses were done separately for the two species.

4.2.2. Food availability from soil seed bank

Soil samples from different months and years were examined and used as indices of seed availability in the soil seed bank. Soil samples were collected during different projects (McNaught 1994, Tischler 1998, McIntyre 2001, see below), including the present study, but the techniques of collection were similar enough to allow robust analysis and comparisons.

Soil samples of April 1994, August 1994, May 1996, October 1996, April 1997, September 1997, September 1999

Soil samples in these months were taken from eighteen long-term plots (9 m^2 area, 3 x 3 metres) on dune slopes at Ethabuka, using a procedure established by McNaught (1994). A bottomless cake tin 20 cm in diameter was used for soil collection. The tin was inserted into the soil to 1 cm (314.16 cm^3) and a piece of cardboard slotted underneath to keep the sample in the tin. The soil was then placed in plastic bags, transported to the laboratory, and sifted into a sieve (0.6 mm) to separate seeds from sand and non-seed material. The remaining portion of the sample was then sifted again through a finer sieve (0.25mm). Both sifted remains were examined under a dissecting microscope and seeds collected, identified to species level when possible, and counted.

Soil samples of April, June, August 1998

Soil samples were collected from two randomly selected dunes at Ethabuka (Tischler 1998). On each dune two transects were marked, one on the crest and one in the swale. On each transect nine sand samples were taken at intervals of 15 m for a total of 36 samples each month. At each sampling point a standard cup of sand was taken from the top 5 cm. The sand was placed in a plastic bag and sorted in the laboratory. There, each sample was

thoroughly mixed, a subsample of 33 cm^3 taken, and the sand sieved through 250 µm gauze. The sieved product was then sorted, all seeds collected and identified to species using the study area reference collection.

Soil samples of March and April 2001

Soil samples were taken using a square tin (16 cm x 16 cm), inserted into the soil to 5 cm (i.e. 1280 cm^3). The collection took place on three different dunes, each separated by approximately 1 km (McIntyre 2001). Soil samples were placed in plastic bags, and sorted in the laboratory with a 500 µm sieve. Seeds smaller than 0.5 mm were not included in the analysis. Husks were probed with forceps to detect viable seeds, and seeds were identified to species when possible.

In order to standardise the data collected on the different occasions, above, the abundance of seed was expressed as percentages (each seed species as a percentage of the total species counted), as volumetric density (number of seeds per cm^3), and species diversity per soil sample. As before, collection periods were divided into the four phases defined for each rodent species.

Correlations were also computed between food resources and plant cover, flower and seed crop indices, and seed abundance from soil samples.

4.2.3. Diet

I analysed a total of eighty-three gut content samples from the two study species. Specimens were collected at Ethabuka over a period of twelve years from March 1990 to December 2001. They were mainly individuals found dead in traps or specimens killed during previous research in 1990-1992 (Predavec 1994a). The specimens were preserved in 10% formalin.

To assess the diet of the two species at different stages of population growth, four phases of different density were chosen from the graphs presented in Chapter 3 and from graphs of capture rates per trap-night to represent high, decreasing, low and increasing population abundance. High phases were characterised as periods when the capture rate was at least 0.09 animals per trap-night, low phases when the capture rate was a maximum of 0.004 animals per trap-night. Increasing and decreasing phases were defined by increments or decrements in the capture rates of 0.001 animals per trap-night outside the high and low

phases. For convenience, I have termed the fluctuations of the rodent populations through the different phases as 'population cycles'. This term, as used in this thesis, should not be taken to imply that the desert rodents I studied have regular population fluctuations or show any dynamical behaviour that is necessarily similar to the predictable fluctuations of some northern hemisphere rodents. For each of the four phases a minimum of ten specimens of each species (five females and five males) was used for gut content analysis. On two occasions the number of gut contents analysed was higher than ten; these were during the decreasing and the increasing phases of *N. alexis*, when eleven and twelve gut samples respectively were analysed. The cumulative number of samples was plotted against the cumulative number of food items to determine the sample size required to give a reliable representation of the diet. This showed that the sample size available for the two species provided a good representation of the diet for most phases, so the results are likely to be representative for each phase period.

The method of diet analysis was a modification of the technique used by Murray and Dickman (1994a). Gut contents were first extracted from the specimens, and then washed with water into a 125 μm sieve to remove the finest particles. Pilot studies of 38 guts showed that analyses of stomach, caecum and faecal pellets usually were equally good in representing the gut's contents. However, to avoid possible biases, the whole content of the gut was always analysed, pooling together the three regions of the gut. After sieving, the contents of the sieve were poured into small Petri dishes, placed over a 50 mm by 50 mm grid and then examined under the microscope at both 40X and 100X magnification. The grid was used to ensure that the entire gut content was observed equally. The individual fragments of digesta were identified to the lowest taxon possible. The unique features of seed husks were used in species identification. A reference collection of seed, plant and invertebrate material created from specimens collected in the study area was used. Insects and other invertebrates were grouped together.

For quantitative analysis, a pilot study (Murray and Dickman 1994a) determined that counts of 120 and 135 dietary particle fragments per each region of the gut for *N. alexis* and *P. hermannsburgensis*, respectively, gave reliable estimates of the overall percentage composition of the different food groups. These sample sizes were raised here to 130 and 145 fragments per gut respectively to increase the accuracy of the analysis. Specimens analysed for this research were completely different from the pilot study. The contents of the 125 μm sieve were placed over the grid and 20 random subsamples were pipetted onto a slide. The slide was then left to air-dry for a few hours and shaken occasionally to avoid

the formation of clumps. It was then observed over the grid at 100X magnification. The food categories were recorded and expressed as percentages. The results are represented graphically as percentage abundance of each food category, and differences between species, sexes, classes of reproductive condition (section 3.2.1), and food categories were tested. Food categories were then grouped into major classes for gross analysis (seeds, fruits, green plant material, invertebrates, other). Seed species were grouped and analysed in major categories representing families, plant types (e.g. forbs, shrubs, grasses, and trees), and whether annual or perennial. Analyses of categories of food items at species-level were defined as fine-scale analyses.

4.2.4. Analyses

4.2.4.1. Relating diet to resource availability

The average number of different food items ingested per individual in any monthly sample was correlated with plant cover for those months to test the hypothesis that diet should not change with plant cover (Model 2, prediction 3). Pearson product-moment correlation coefficients were used for all correlations in this chapter. *P*-values were adjusted using the Dunn-Sidak correction for multiple comparisons (Sokal and Rohlf 1995). Percentage plant cover was arcsine-transformed and the average number of food items was log-transformed in order to meet the assumptions of normality and homogeneity of variances. In order to further test the same hypothesis, the overall diet of the two species for each of the four phases was compared graphically with average total cover for these periods.

To test prediction 3 of Model 3 (diet should change with changing food resources), the average number of different food items ingested per individual rodent in any sample month, was correlated with seed crop index, flower crop index, and seed abundance from soil sample for those months. Changes in diets were also compared with changes in the different food resource categories (plant cover, seed abundance from plant survey, seed abundance from soil samples, flower abundance) during the four time periods. A proportional similarity index (PSI) (Feinsinger *et al.* 1981) was used as a measure of similarity between gut contents and food categories. This kind of index has been often used to measure niche overlap or community similarity (e.g. Colwell and Futuyma 1971, Whittaker 1975), but it

actually measures more accurately the actual area of intersection between two frequency distributions (Feinsinger *et al.* 1981). The index is as follows:

$$PS = 1 - 0.5 \sum_i | p_i - q_i | = \sum_i \min (p_i, q_i)$$

where p_i is the proportion of resource items in state *i* out of all items used in one phase, and q_i is the proportion of *i* items available. This index ranges from min q_i (minimal area of intersection, minimal overlap) to 1 (maximal area of intersection, maximal overlap).

To further compare food availability with food eaten by the two species, a rank analysis modified by Johnson (1980) was applied. The average abundance of each seed species and family identified in the gut contents was compared with the average abundance of the same seed species and family identified in plant surveys and soil samples. Because the three sets of data were expressed in different ways (i.e. indices, percentages, volumetric density) the only way to compare them was by using rankings. Following the methodology described by Johnson (1980) the three sets of data were first expressed as percentages. Then each species within each data set was ranked from the most preferred/abundant (1) to the least preferred/abundant (n). Ties were expressed by summing 0.5 to obtain equal ranks. Ranks of common species were extracted from the food resource data sets and compared with the ranks of the same species in the diet as follows:

$$T_i = \text{Rank } U_i - \text{Rank } A_i$$

where T_i is the difference between rank of usage of species *i* (Rank U_i) and rank of availability of species *i* (Rank A_i). Consequently, an avoided species will be expressed by a big positive number (big Rank U_i and small Rank A_i) and a selected species by a big negative number (small Rank U_i and big Rank A_i). Successively, the differences between all species are ranked again, but this time indicating the least preferred with 1 and the most preferred with n. A problem with this type of representation of selectivity arises when a species is present in the diet but not in the plant survey or soil samples (e.g. animals foraging outside the area of data collection, bias due to plant survey, bias due to diet analysis). In this situation the selection for a less preferred species can be overestimated.

To test the hypothesis that diet should change with food resources (prediction 3 of Model 3) multivariate analyses were applied on fine- and gross-scale categories of food items to compare the composition of the four categories of food resources (plant cover, seed abundance from plant surveys and soil samples, and flower abundance) between

phases. Because phases did not coincide exactly for the two rodent species, the analyses were carried out with two factors (phases and rodent species). Non-metric multidimensional scaling (MDS), analysis of similarities (ANOSIM) and similarity terms (SIMPER) procedures (see below) were performed on the four food categories to detect the main components of dissimilarity between population phases of the two rodent species. For the SIMPER analysis the abundance of seeds in the soil samples was expressed as mm^3 to avoid large decimal figures and ease the data readings.

The other way I tested prediction 3 of Model 3 was to analyse the overall diet of the two species during different population phases. Multivariate analyses were again used to compare fine and gross dietary composition between phases, animals in different reproductive condition, rodent species and sex. Similarities were calculated between samples using the Bray-Curtis similarity index (Bray and Curtis 1957). This method produces a symmetric triangular matrix of similarity values. A two-dimensional ordination of the samples was produced using MDS (Clarke and Green 1988). MDS relies on the rank order of similarities between samples, and thus there are no restrictive assumptions of normality or equality of variances or covariances among variables (Anderson and Underwood 1994, Scott *et al.* 1999). The difference between the rank-order distances between samples in the original similarity matrix and the rank-order distances represented by the two-dimensional MDS of those samples is expressed by a stress coefficient. MDS produces a visual representation of the data, and stress values of less than 0.20 generally lead to an interpretable MDS pattern (Clarke 1993, Scott *et al.* 1999).

ANOSIM was used to test for differences in the composition and abundance of food items between population phases, reproductive condition, rodent species, and sex. ANOSIM establishes biological differences between samples and includes a non-parametric randomisation test of the factors examined (Clarke and Green 1988). SIMPER was used to identify the importance of fine or gross food item variables within predefined groups (phases, rodent species, sex and reproductive condition). This exploratory method calculates the average similarity between variables in predefined groups evident from MDS and ANOSIM. The average similarity is then broken down into separate contributions for each food item to give the average contribution to similarity as a percentage for each food item within each group. In pilot tests, the sexes did not show any significant difference and were therefore grouped in later analyses. All the analyses were performed including the plant material that could not be identified in gut samples, even

though it in some cases represented a large percentage of the food items identified in the guts. All multivariate analyses were carried out with PRIMER V.5 (Clarke 1993).

In order to detect differences in food items eaten by the rodent species, and by pregnant females and other adults during the different population phases, the Mann-Whitney test was used to compare foods in the fine and gross food categories. This non-parametric test was chosen because some food categories had zeros in all replicates, and arcsine-transformation was unable to improve homogeneity of variances.

To further assess dietary differences between the two rodent species, diet niche breadths and overlaps were calculated for each phase. Levins' measure (B) (Krebs 1989) was used, as follows:

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where p_i is the fraction of food item i in the diet ($\sum p_i = 1$) and n is the number of food items. This measure varies between 1 and the total number of food items found in the diet. If only one food item is eaten the niche breadth is 1. The more evenly the different food items are consumed, the higher the niche breadth (Wathne *et al.* 2000). The niche breadth expresses to what degree a consumer is a generalist or a specialist. A generalist will often exploit various prey items regardless of species identity, while specialists are very species selective. Generalists are characterised by high values of niche breadth measurements, whereas specialists have low values of niche breadth (Wathne *et al.* 2000). To calculate dietary niche overlap between the two rodent species two indices of similarity were used and compared to minimise biases associated with each type of measurement. The indices were calculated for both fine categories and gross categories (seeds, plant material, invertebrates, fruits, and other). Parasites found in the gut contents represented a category that was analysed separately. Pianka's index (O_{jk}) (Pianka 1973, Wathne *et al.* 2000) was calculated as follows:

$$O_{jk} = \frac{\sum_{i=1}^{n} (p_{ij} \times p_{ik})}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where O_{jk} is Pianka's measure of niche overlap between species j and species k; p_{ij} is the proportion of food item i in relation to the total amount of food items ingested by species j; p_{ik} is the proportion of food item i in relation to the total amount of food items ingested by species k, and n is the total number of food items. Pianka's index is symmetrical, thus the overlap between species j and species k is identical to overlap between species k and j. The

index ranges from 0 (no overlap) to 1 (complete overlap). Wallace (1981) considered that values higher than 0.6 represent a biologically significant niche overlap for the resources examined. The second measure of similarity was the percentage similarity, also called the Renkonen index (Renkonen 1938). In spite of its simplicity, Krebs (1989) stated that this index is one of the best quantitative similarity coefficients available, because it is relatively unaffected by sample size and by species diversity. To calculate this measure of similarity, each sample must be standardised as percentages so that the sums of relative abundances equal 100% in each sample. The index was calculated as follows:

$$P_{12} = \sum_{i=1}^{n} (\min p_{1i}, p_{2i})$$

where P_{12} is the percentage similarity between sample 1 and 2, p_{1i} is the percentage of species i in sample 1, and p_{2i} is the percentage of species i in sample 2, n is the total number of resource states. This index ranges from 0 (no overlap) to 100 (complete overlap).

4.2.4.2. Relating food resources to rainfall

In order to test the first and the second predictions of Model 2, the average monthly plant cover and plant cover species diversity were correlated with the modified monthly CDMR of Chapter 3 and with the capture rates per trap-night of the two rodent species at Ethabuka. In order to recognise lag effects, plant cover was also correlated with the modified CDMR values and capture rates for each species over the previous 12 months. Arcsine and log-transformations were used to improve the normality and homogeneity of the variances. Time-lagged calculations and transformations were applied to all the following correlations in this chapter. Fine categories (individual plant species) were used in these and in the following analyses.

To test the first prediction of Model 3 (other than with plant cover, as already reported above), the modified monthly CDMR was also correlated with the monthly seed crop index, the monthly flower crop index, the monthly seed abundance in the seed bank, and the species diversity of each of these food resources. The second prediction of Model 3 was tested by correlating capture rates per trap-night of the two species with the seed crop index, the flower crop index, seed abundance in the seed bank, plant cover, and the species diversity of each of these food categories.

4.3. Results

4.3.1. What food is available: food resource analyses from plant surveys and soil samples

A total of 196 plant species was identified from the plant surveys over the twelve-year study period. Amongst them, 114 were recorded as carrying flowers and 120 as carrying seeds during surveys. A total of 53 seed species was found in the soil samples. Figures 4.1 to 4.4 show total monthly abundances of the four categories of food resources potentially available to rodents, expressed in percentages both with and without the contribution of the dominant species at the site, spinifex *Triodia basedowii*. The main increment in cover during the study period was clearly due to spinifex; in some months most samples of seeds and flowers also were dominated by spinifex. High productivity of seeds and flowers, especially spinifex, was recorded during the Increasing phase for rodents (October 1999 to October 2000) that preceded the peaks of 2001, while the seed and flower abundance during this latter period was relatively low. However, during the peaks in productivity and rodent numbers of 2001, other species mostly comprised the seed and flower crops, while the highest recorded cover abundance during 2001 was mostly due to *T. basedowii*. Overall, spinifex represented the largest quantity sampled in all the four food categories (Figure 4.5), followed by different species depending on the category (e.g. *Aristida contorta*, *Trachymene glaucifolia*, *Euphorbia drummondii*, *Calandrinia balonensis*). The patterns of abundance of seeds on plants and in soil samples showed little consistency, with some species (e.g. *A. contorta*) being more abundant on plants, and others (e.g. *T. glaucifolia*) being most abundant in soil samples (Figure 4.5).

4.3.2. What rodents eat: gut content analysis

4.3.2.1. Overall diet

A total of 65 different food items was identified in the gut contents of *N. alexis* over ten sample months, and 49 food items were found in the gut contents of *P. hermannsburgensis* over thirteen months. For analysis, unknown material (unknown plant tissues, fruits and seed species) was then compacted under single categories for both species, resulting

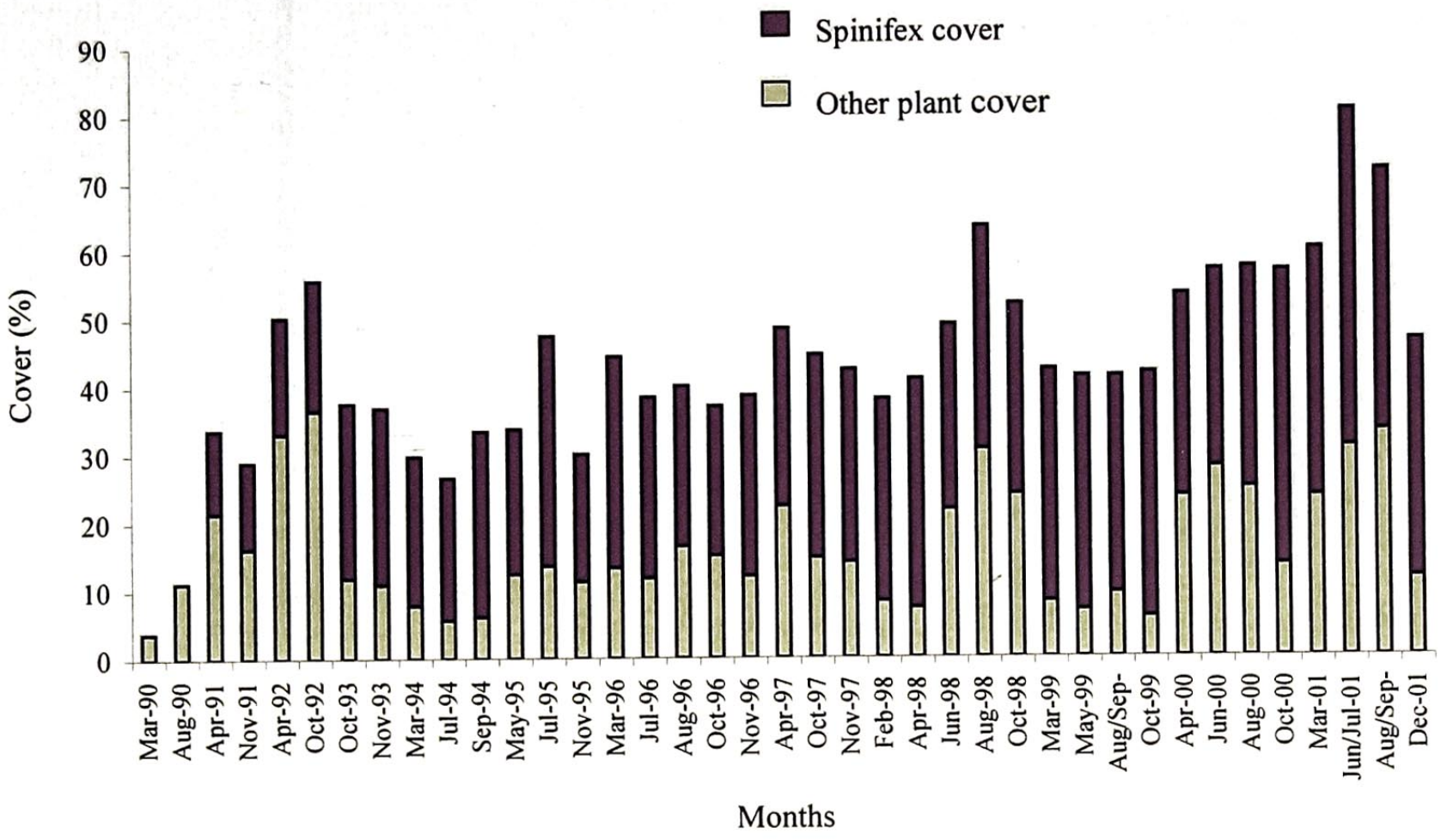


Figure 4.1. Monthly total cover of vegetation, with and without spinifex.

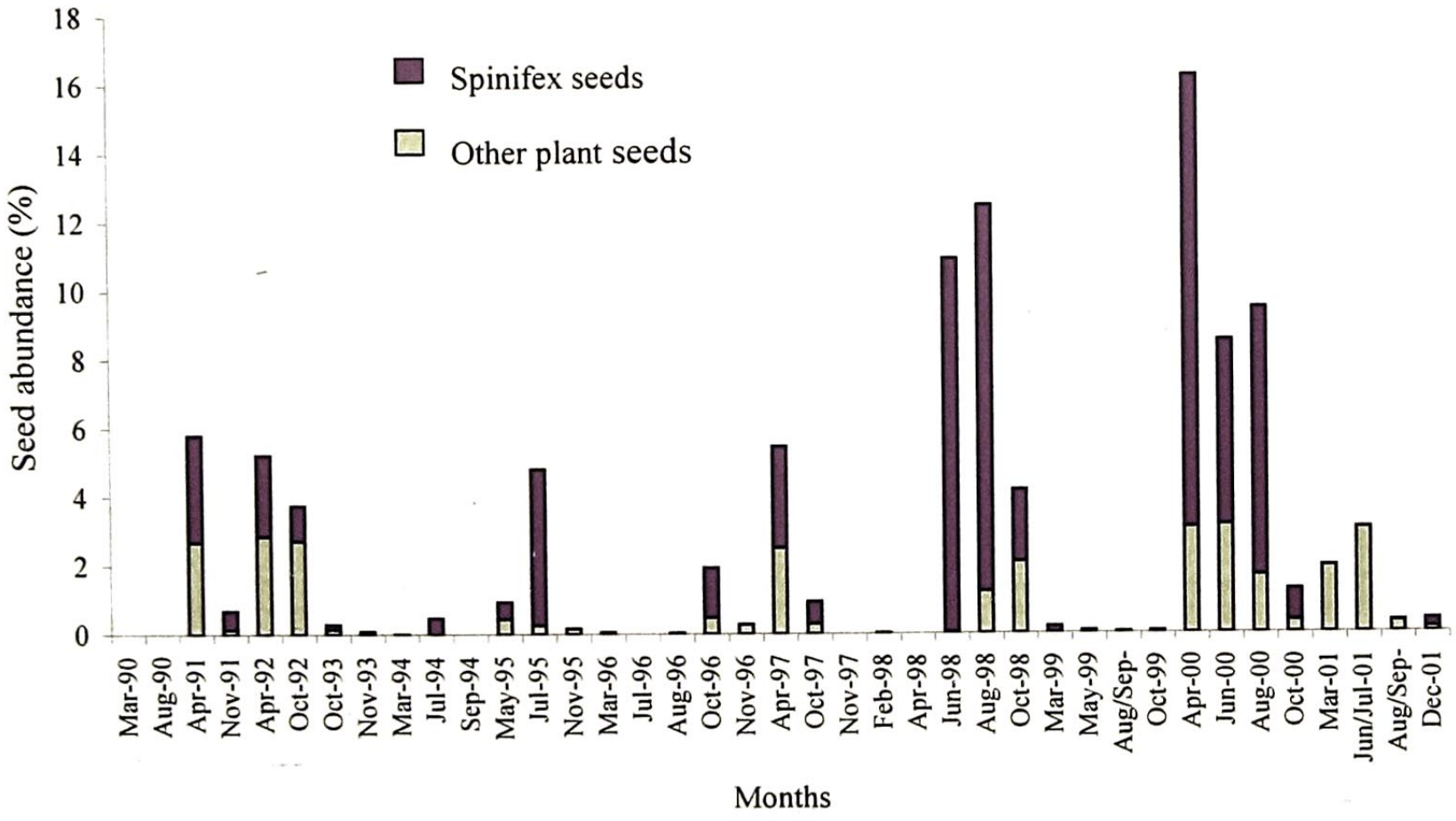


Figure 4.2. Monthly seed abundance on plants, expressed as percentage of the total seed abundance over the study period.

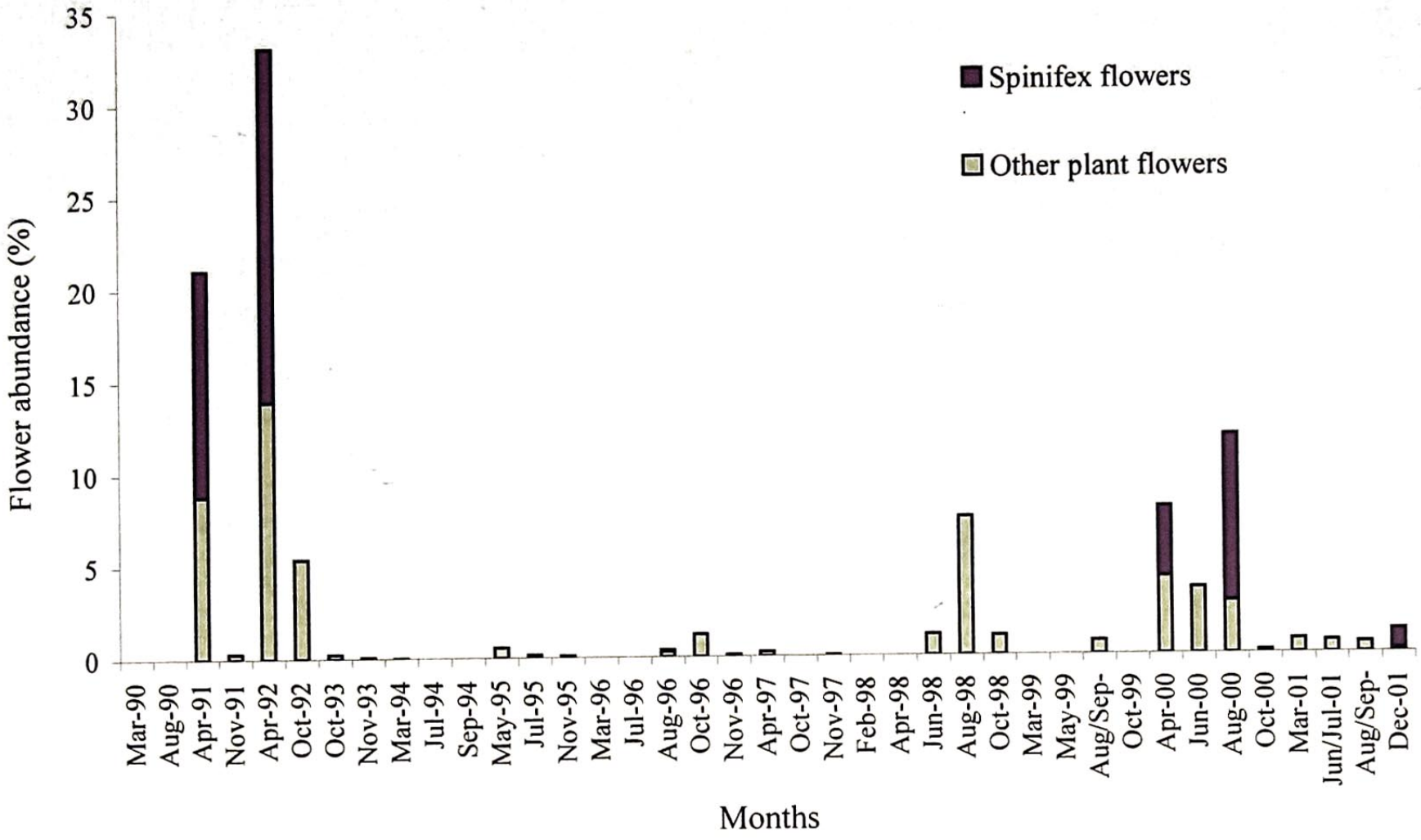


Figure 4.3. Monthly flower abundance expressed as percentage of the total flower abundance over the study period.

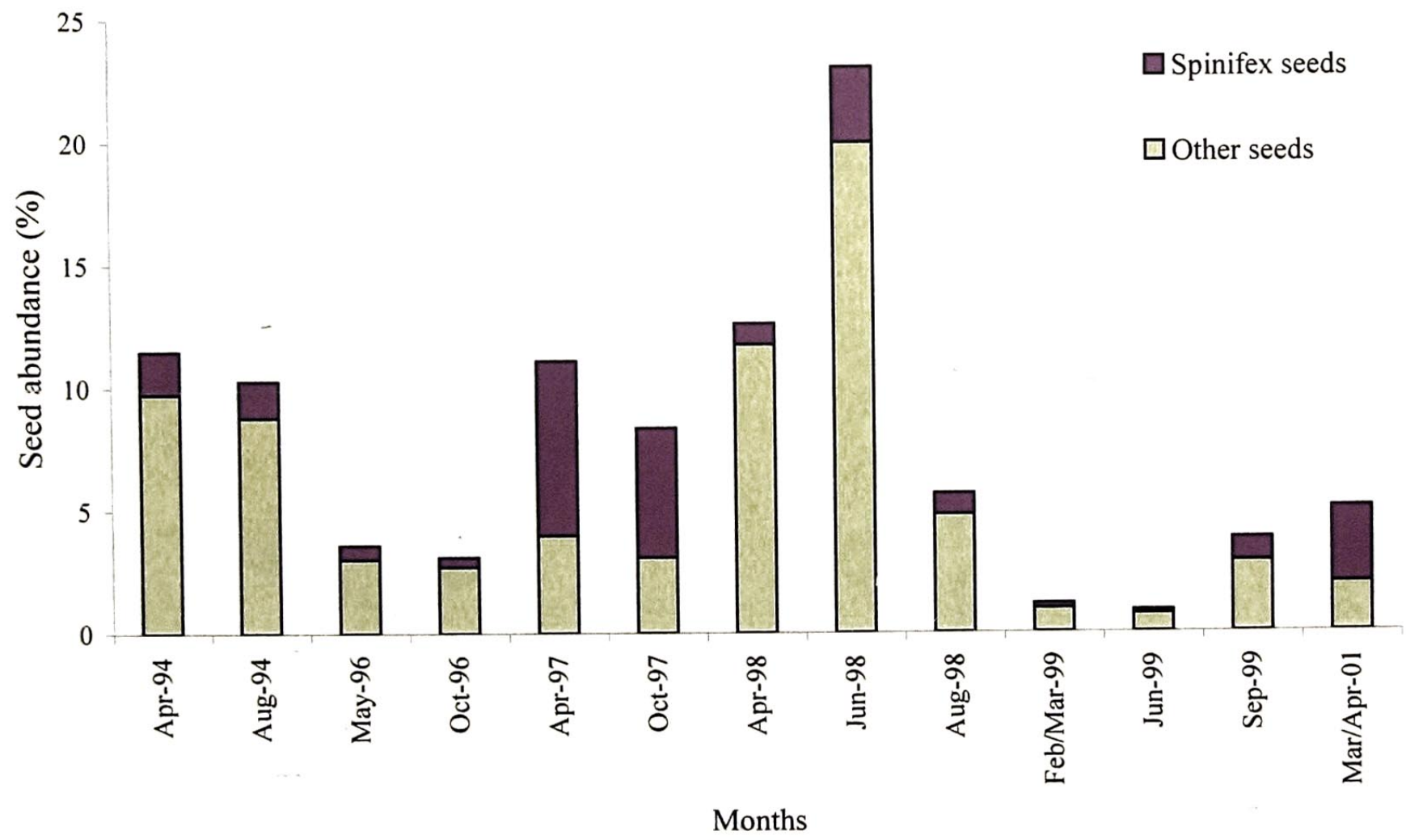
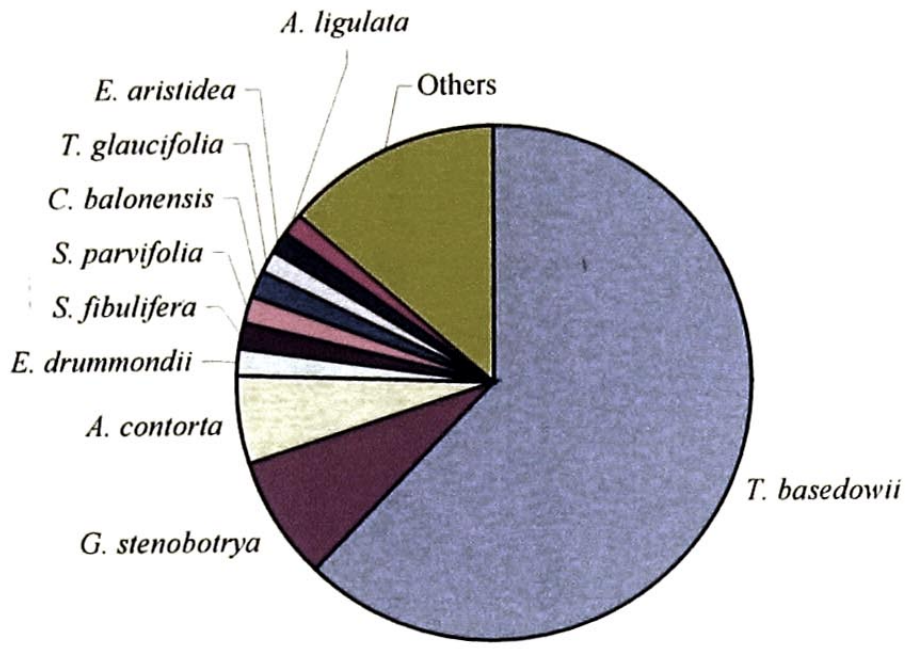
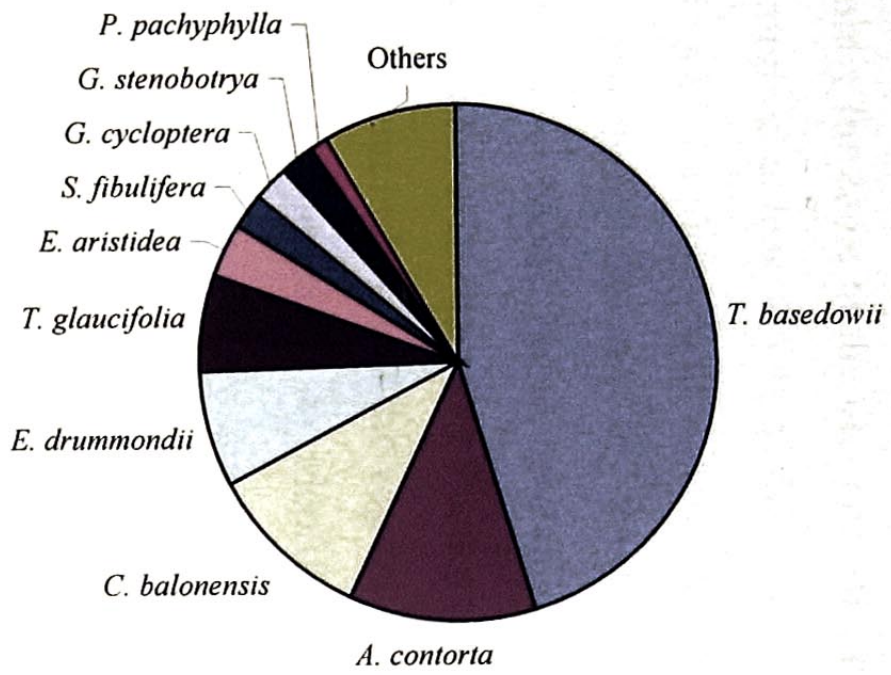


Figure 4.4. Monthly seed abundance in soil samples, expressed as percentage of the total seed abundance over the study period.

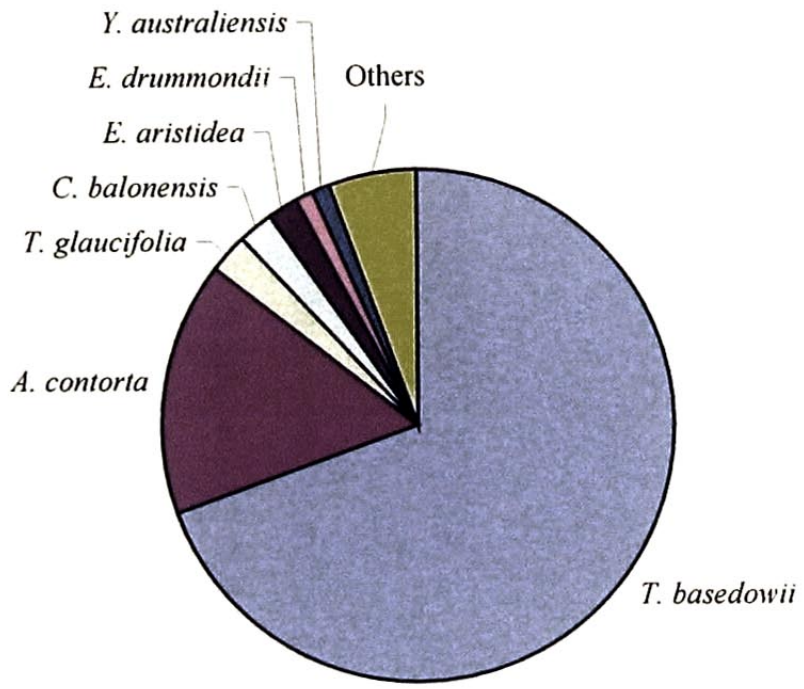
Main plant cover species (abundance > 1%)



Main flower species (abundance > 1%)



Main seed species on plants (abundance > 1%)



Main seed species in soil sample (abundance > 1%)

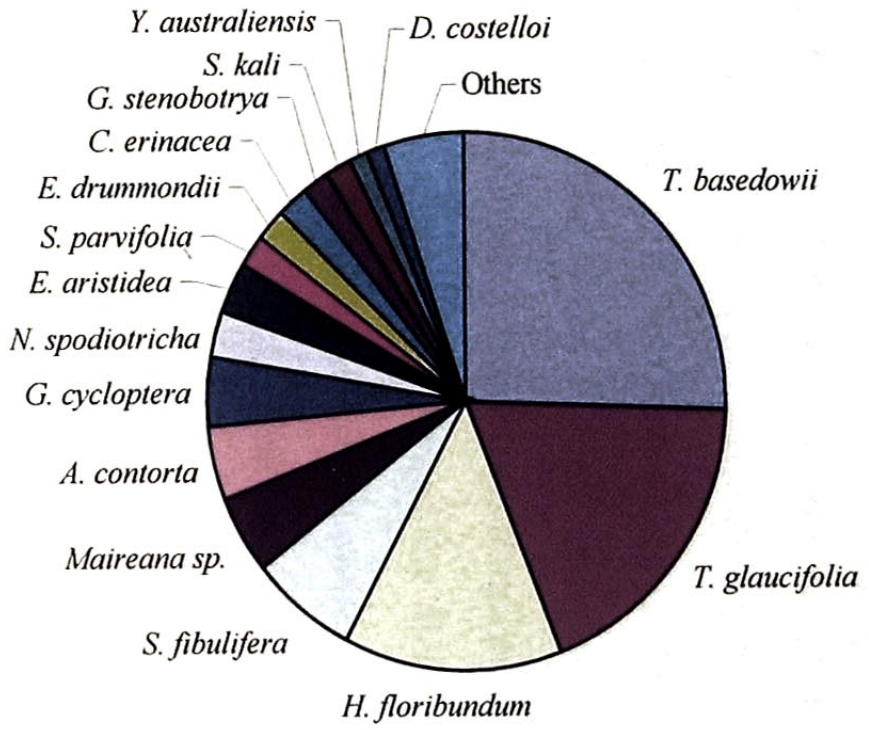


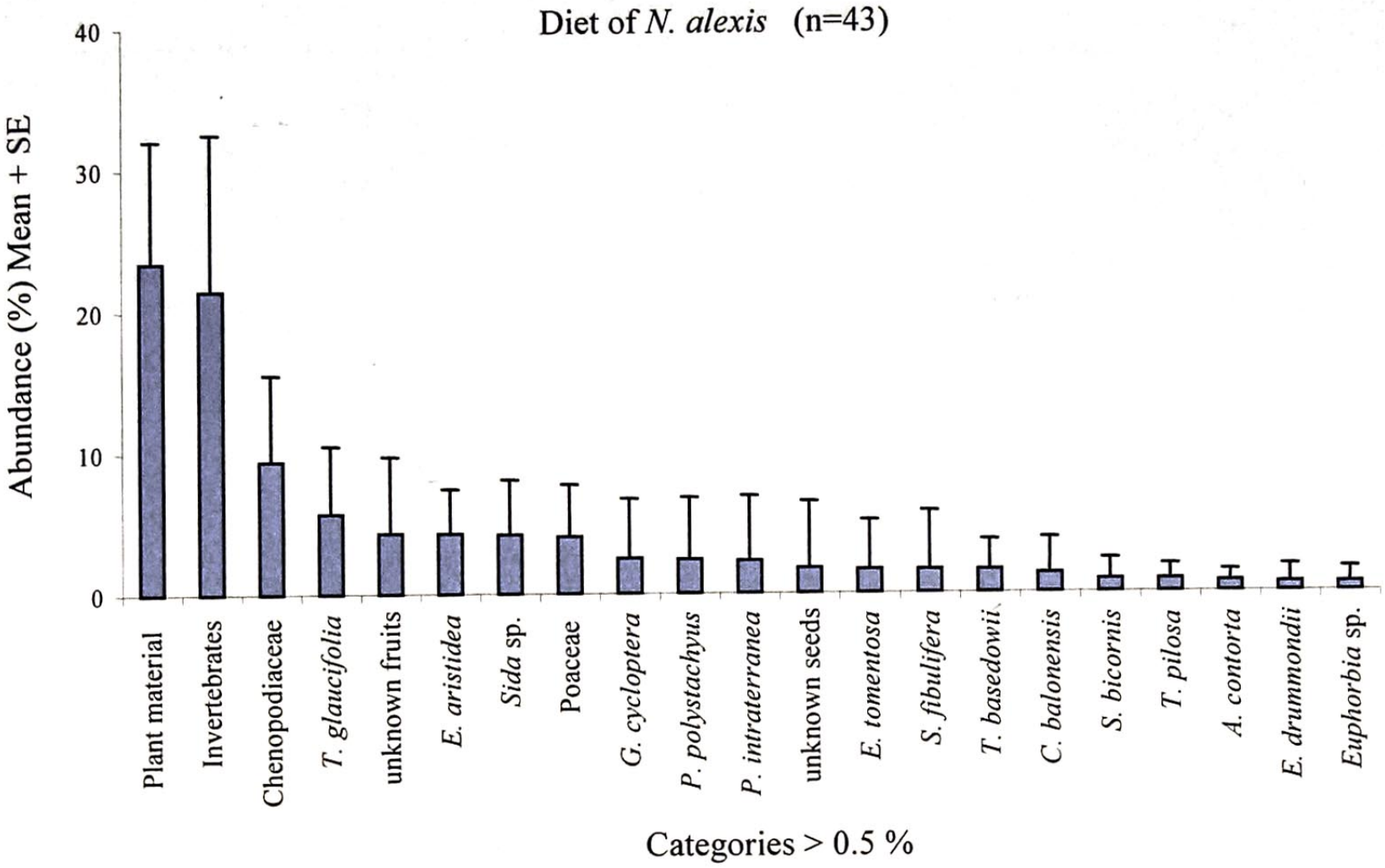
Figure 4.5. Main plant species in the four categories of food resources available to rodents, averaged over surveys from 1990-2001. The species shown have abundances > 1%. The remaining species are summed together and indicated as "others". Full names of plant species are given in Appendix 3 (Table 1).

in a final total of 42 and 37 food items for *N. alexis* and *P. hermannsburgensis* respectively. Compaction was justified because these unknown food items were consistently the same in the diet analysis. In Figure 4.6 are presented the food categories that comprised at least 0.5 % of the diet for both species. Invertebrates constituted a large proportion of the diet of both species, as Murray and Dickman (1994a) also found in their study. Food items consumed by the two species were similar, even if their abundance varied between species. Fruits were an exception, being consumed in quite high abundance only by *N. alexis*. The category Plant material represents a conspicuous part of the diet of both species and includes all the vegetation fragments (stems, plant tissues, unknown husks etc.) that were impossible to identify because of lack of particular characteristics or because they were too finely chewed. Some plant remains were identified at family level by their diagnostic features (e.g. Chenopodiaceae, Poaceae), but it was impossible to describe them at species level (Figure 4.6).

A graphical analysis of the relative abundance of the gross categories of food eaten by both species during different population phases shows that seeds constitute a dietary staple for both species, but also that their abundance in the diet varies with cycle phase (Figure 4.7). Invertebrates, Plant material and even Fruits predominate in the diet at times. Parasites are presented in this gross depiction as another category found in the rodent guts, even though they are not a food item. Parasites in the guts can represent indirect information on the health status of the rodents during population fluctuations, and thus are worthy of consideration. However, this category was analysed separately (see section 4.3.6).

4.3.2.2. Are the diets of the two species different during different population phases?

In analyses of gross food categories (plant family, type, whether annual/perennial, and invertebrates) some dietary differences were observed between the two species in different population phases. Seeds from some plant families were consumed significantly more by *N. alexis* than *P. hermannsburgensis* (e.g. Goodeniaceae, Chenopodiaceae, Poaceae, and Malvaceae), while *P. hermannsburgensis* generally consumed more seed of Apiaceae (Figure 4.8). In Figure 4.9 the analysis has been done by dividing plants by type (e.g. shrubs, forbs, grasses, etc.). The two rodent species made differential use of seeds from some plant types during different population phases (Forbs, Fruits, Shrubs, and Plant material). However, there was little consistency in food categories taken between phases,



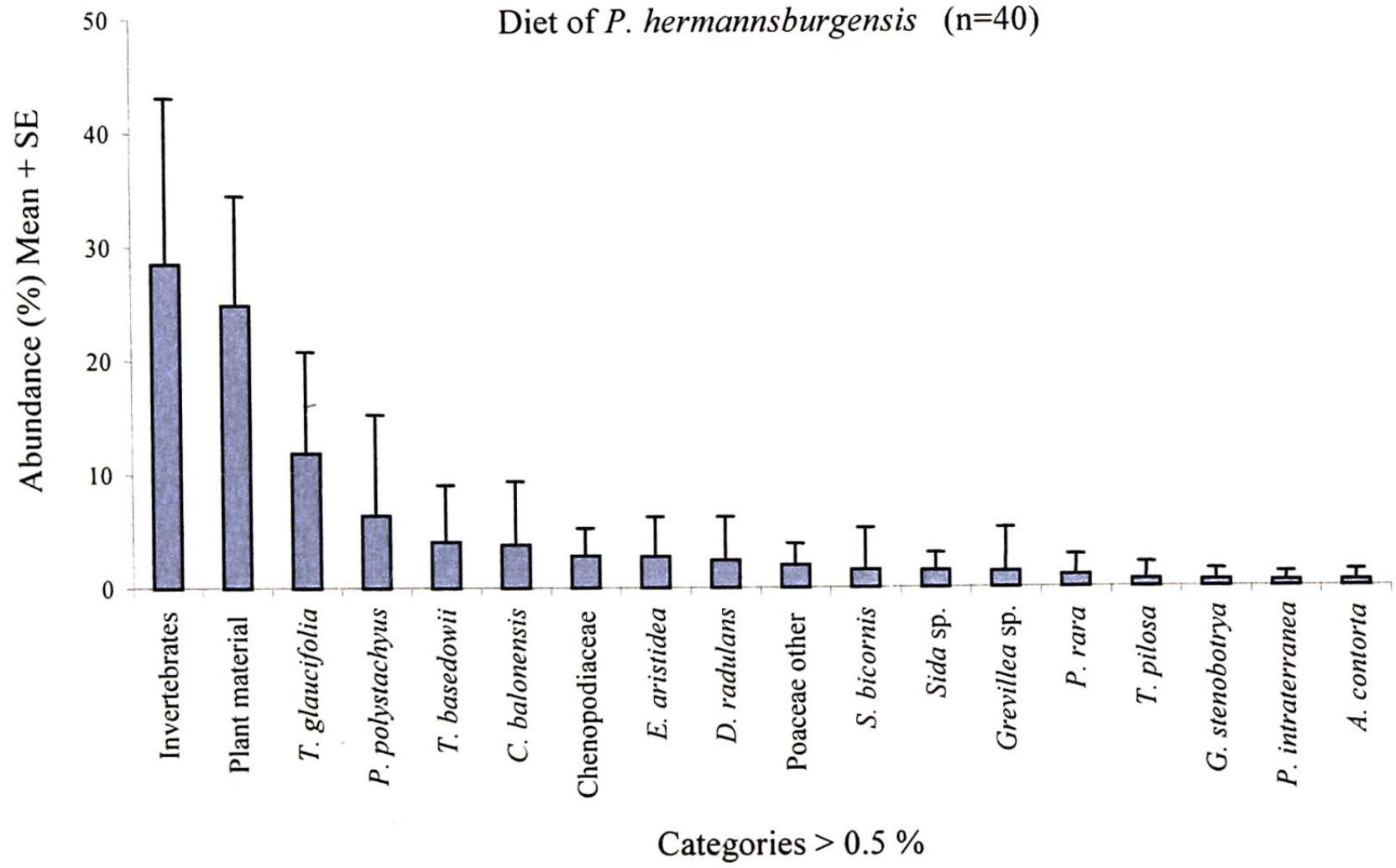


Figure 4.6. Main food categories (% > 0.5 based on counts of dietary particle fragments) in the diet of *N. alexis* and *P. hermannsburgensis*. Full names of plant species are given in Appendix 3 (Table 1). Except for the categories 'Invertebrates', 'plant material', and 'unknown fruits', all species names refer to seeds.

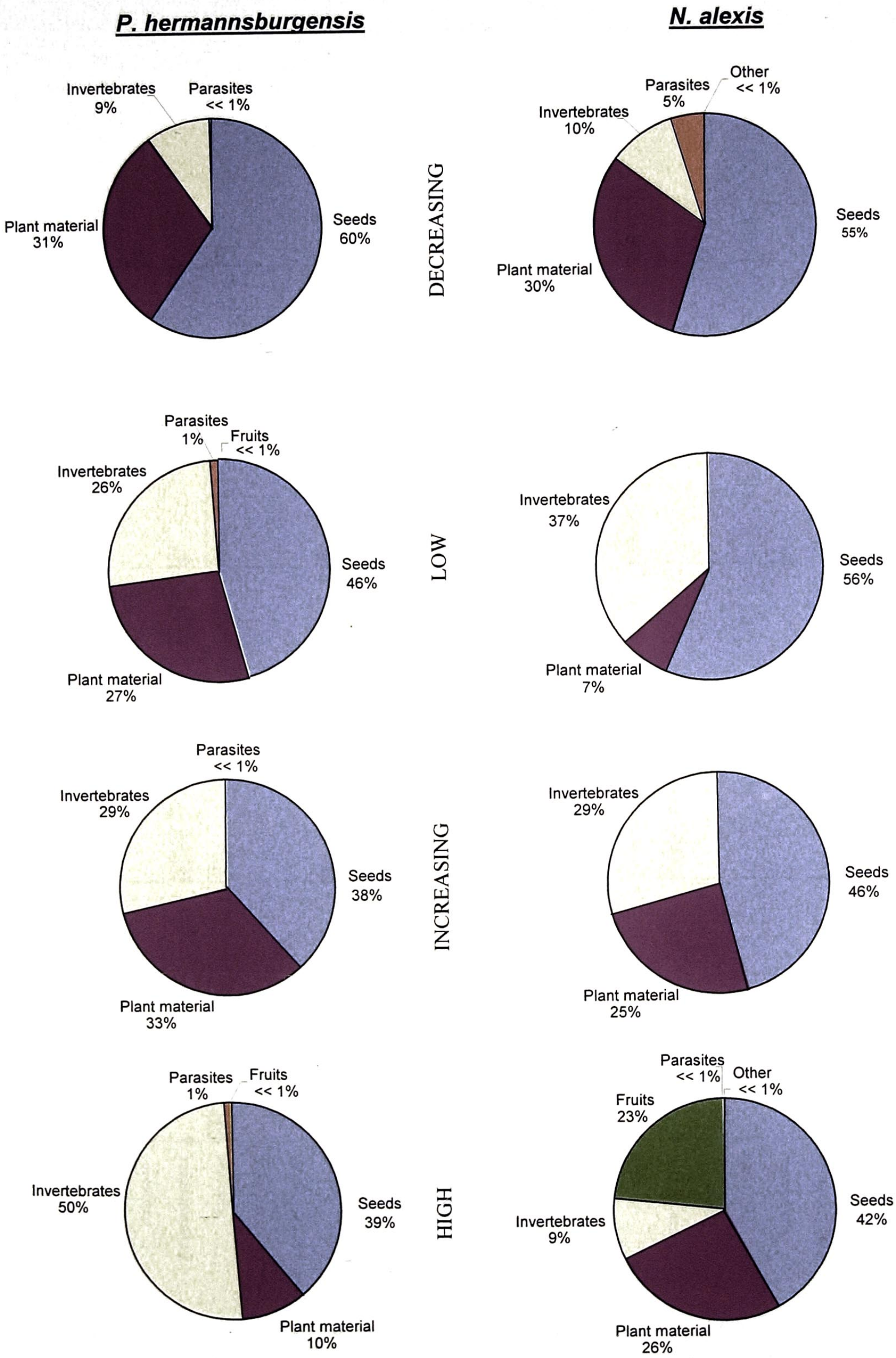


Figure 4.7. Gross categories of food present in the diet of *N. alexis* and *P. hermannsburgensis* in four phases of their population cycle. Percentages indicate the relative abundance of each category.

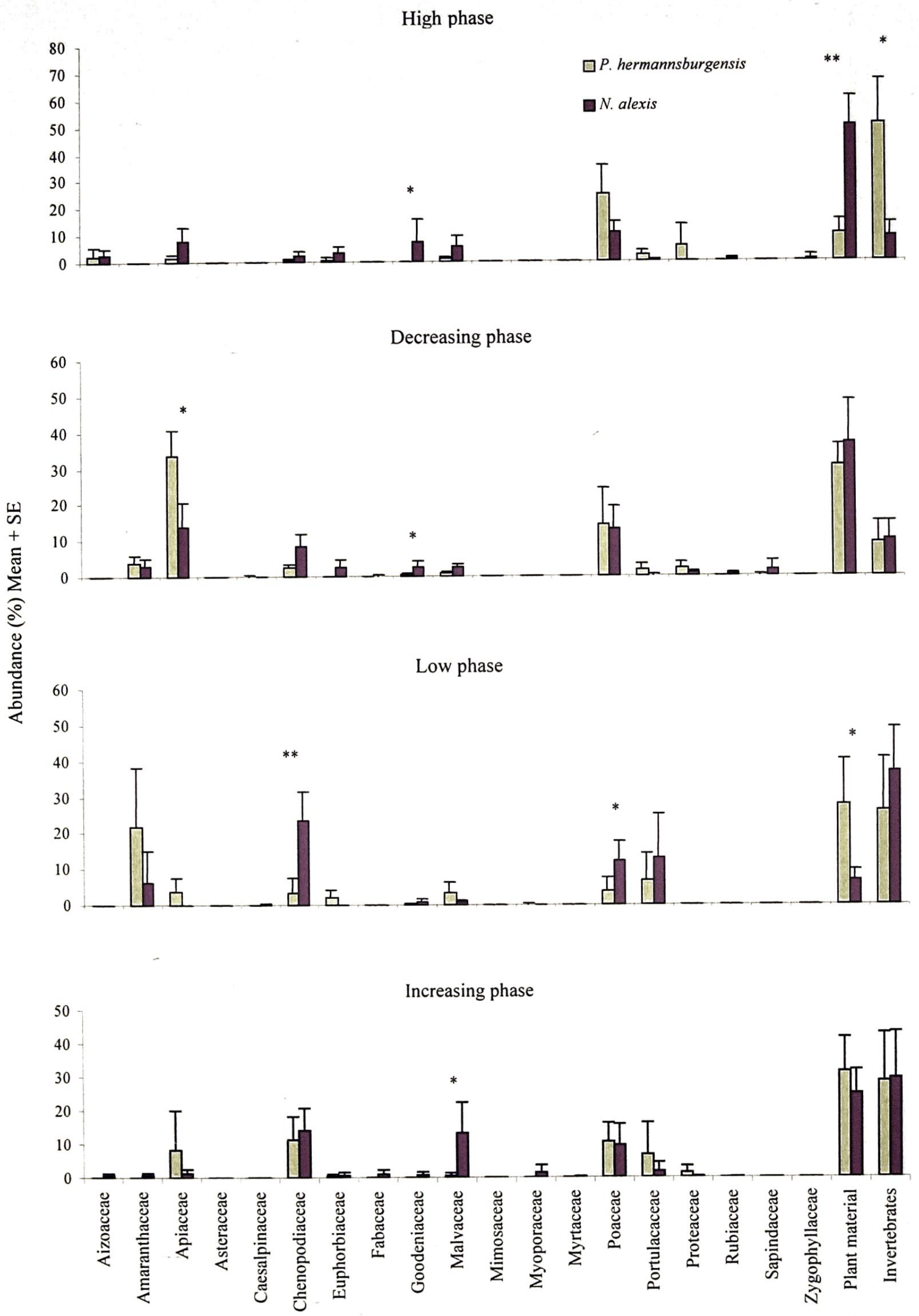


Figure 4.8. Diets of *N. alexis* and *P. hermannsburgensis*, based on counts of dietary particle fragments aggregated into gross food categories (plant family, unidentified plant material and invertebrates), during four phases of their population cycles. Dietary differences were tested by the Mann-Whitney test. * $P<0.05$, ** $P<0.01$.

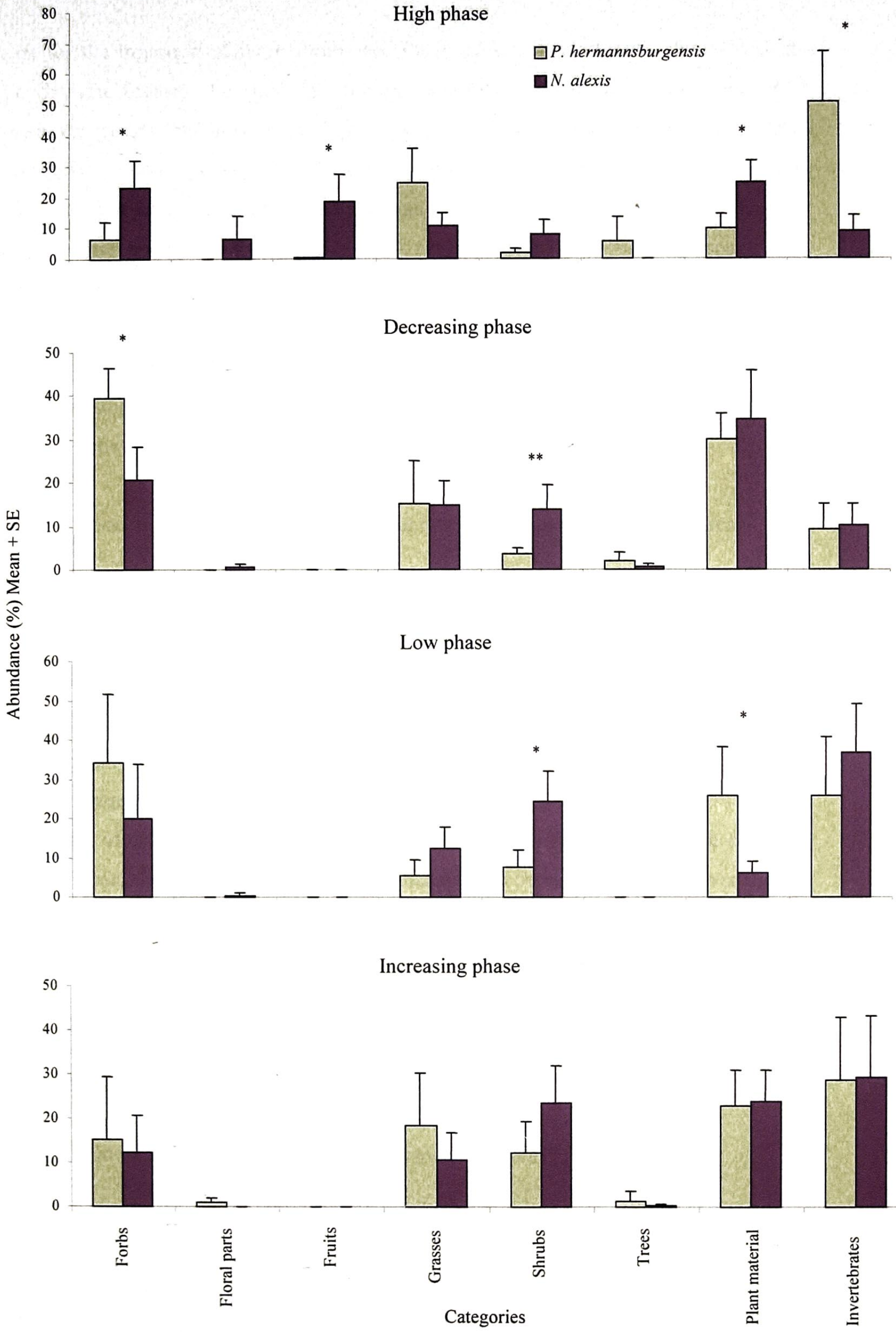


Figure 4.9. Diets of *N. alexis* and *P. hermannsburgensis*, based on counts of dietary particle fragments aggregated into gross food categories (plant type, unidentified plant material and invertebrates), during four phases of their population cycles. Dietary differences were tested by the Mann-Whitney test. * $P<0.05$, ** $P<0.01$.

except for the ingestion of more shrub seed by *N. alexis*. Invertebrates, shown with the same data in Figures 4.8 and 4.9, formed a greater proportion of the diet of *P. hermannsburgensis*, but only in the high population phase. Further dietary comparisons showed that perennial seeds were consumed equally by the two species over the four phases. Seeds of annual and short-lived perennial plants were consumed more by *N. alexis* during the High and the Low phases (U=93.00, P=0.001, U=87.00, P=0.005, respectively), while *P. hermannsburgensis* consumed more seed from annual/biennial plants during the Decreasing phase (U=19.00, P=0.011).

The species-level dietary results are presented in Appendices 1 and 2 (Figures 1 and 2), and indicate some differences in seed species ingestion between the two rodent species, but little consistency between population phases.

4.3.2.3. Do rodent diets change with plant cover during different population phases?

The average number of different items represented in the diet per individual in any month showed no correlation with plant cover (r=0.501 for *N. alexis*, and r=-0.279 for *P. hermannsburgensis*, P>0.05) for those months, thus supporting the prediction that diet should not change with plant cover (Model 2, prediction 3). In Figures 4.10 and 4.11 the overall seed diet of the two species during each of the four population phases is presented with the average total vegetation cover for these periods. It appears clear from these figures that the diets of the two rodent species changed during the different phases with changing plant cover, but not in a linear way, because increases or decreases in plant cover did not necessarily result in increases or decreases in the range of seeds eaten. The greatest range of seeds eaten was recorded during the Decreasing and Increasing population phases for *N. alexis* (Figure 4.10), and the High, Decreasing and Increasing phases for *P. hermannsburgensis* (Figure 4.11), whereas the most abundant cover occurred during the High and Increasing phases for both species.

4.3.2.4. Do rodent diets change with changes in food resources?

Strong correlations were found between seed and flower crop indices and the mean number of different food items eaten by individual *N. alexis* (prediction 3 of Model 3) (r=1.00, P<0.001, with 6-month lag and r=1.00, P<0.001, with 7-month lag respectively). However, the results of these correlations should be viewed with caution because of the

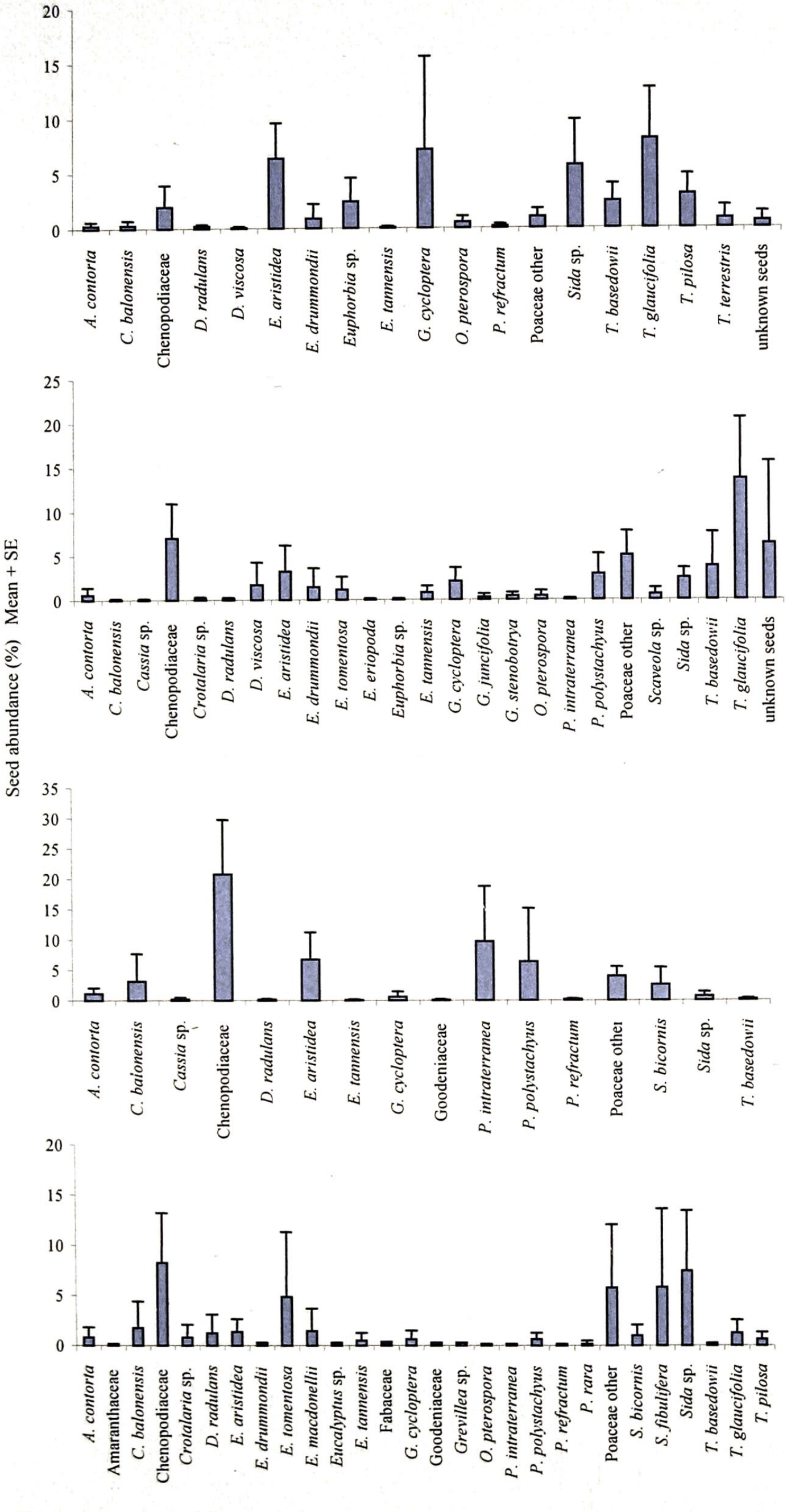


Figure 4.10. Graphical comparison of the overall diet (excluding invertebrates) of *N. alexis* with average total plant cover for each phase. Full names of plant (seed) species are given in Appendix 3 (Table 1).

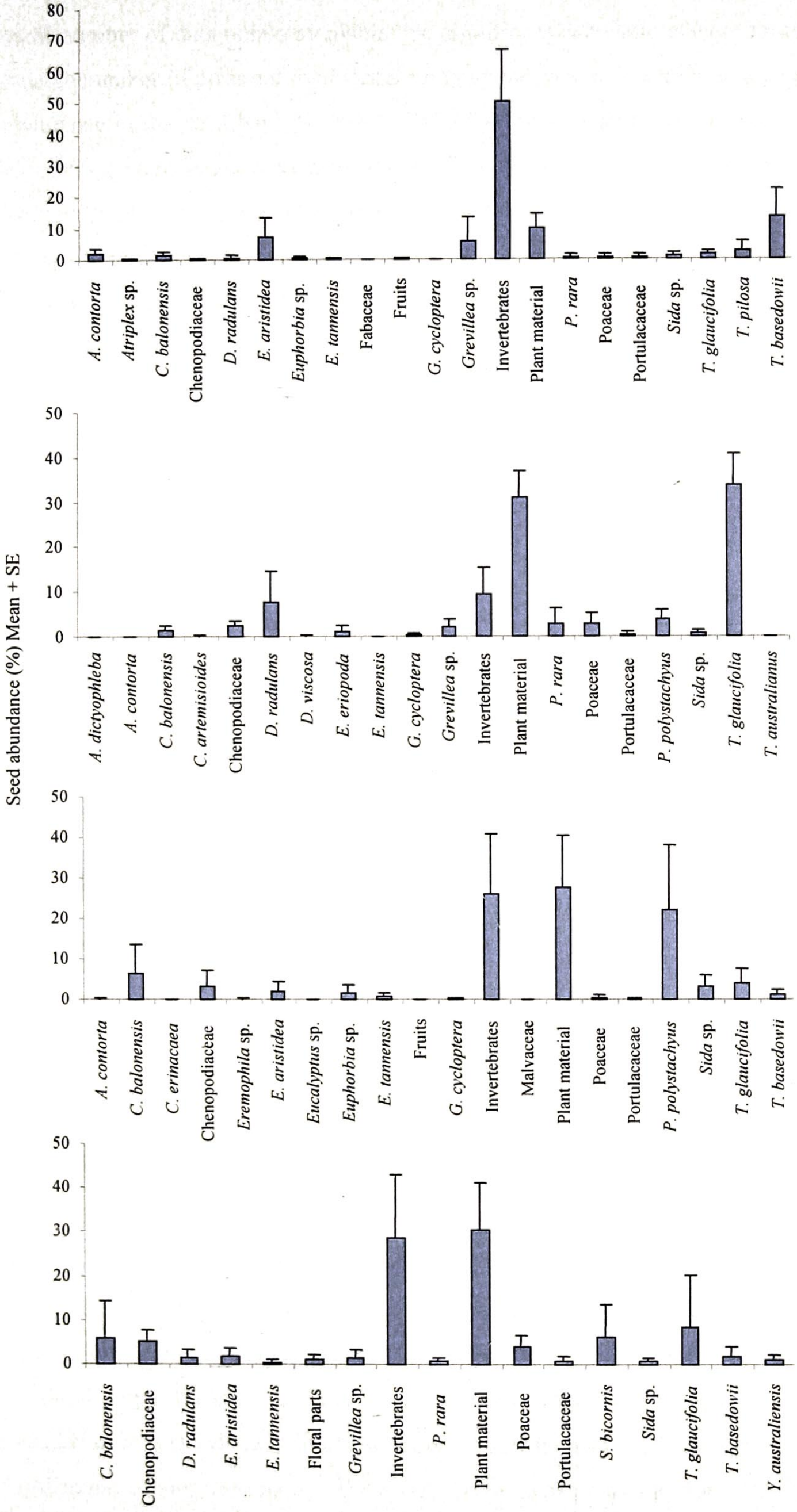


Figure 4.11. Graphical comparison of the overall diet (excluding invertebrates) of *P. hermannsburgensis* with average total plant cover for each phase. Full names of plant (seed) species are given in Appendix 3 (Table 1).

small number of data points available. No significant correlations were found between the average number of different food items eaten by individual *N. alexis* in any month and seed abundance in the seed bank (r=0.001, P>0.05). For *P. hermannsburgensis*, no significant correlations were found between seed and flower crop indices and the average number of different food items in the gut contents (r=-0.800 and r=-0.748, P>0.05 respectively), but a strongly significant correlation was observed between seed abundance in the seed bank and the average number of food items in individual gut contents (r =1.00, P<0.001, with a 7-month lag).

Table 4.1 shows the similarity (PSI) of gut contents with the four main categories of food resources available (plant cover, flower crop, seed crop from plant survey and seed crop from soil samples), and reveals little evidence of a consistent pattern between different population phases or between the two species.

Table 4.1. Comparison of the gut contents with each of the four food categories available to the two rodent species in the four population phases. Similarities are calculated using the PSI (proportional similarity index). H, high phase, D, decreasing phase, L, low phase, and I, increasing phase. Phases have been derived from capture rates of the two rodent species.

Phases	**Cover vs gut contents**		**Flower index vs gut contents**		**Seeds from plant survey vs gut contents**		**Seeds from soil samples vs gut contents**	
	N.alexis	*P. hermann.*	*N.alexis*	*P. hermann.*	*N.alexis*	*P. hermann.*	*N.alexis*	*P. hermann.*
H	0.162	0.469	0.106	0.123	0.060	0.259	0.287	0.617
D	0.198	0.032	0.242	0.083	0.205	0.108	0.465	0.269
L	0.101	0.072	0.194	0.288	0.058	0.086	0.151	0.165
I	0.120	0.079	0.185	0.283	0.156	0.151	0.193	0.474

The largest overlaps between diet and food resources were observed for seeds from soil samples, with the greatest similarity being during the High phase for *P. hermannsburgensis* (PSI=0.617). With the exception of the overlap value between gut contents and plant cover in the High phase for *P. hermannsburgensis* (PSI=0.469), all other overlap values between gut contents and food categories other than soil seed bank were very modest. Plant cover appears to have little effect on diet between phases, while the other food categories exhibited large differences in PSI. In general, rodents fed little on plant material (vegetation cover), whereas their foraging on flowers and seeds fluctuated, with maximal exploitation of soil seed banks. However, the general pattern appeared to be one of little similarity between diets and food resources.

4.3.2.5. What food is available and what is selected: usage of food resources by the two rodent species

Patterns of dietary selection were slightly different for some seeds that were available on plants and in the seed bank (e.g. *Scaveola* sp. for *N. alexis*, *Dodonaea viscosa* for *P. hermannsburgensis*), but the general pattern of seed selection was similar (Tables 4.2 and 4.3). Certain seeds, such as *Grevillea* spp. and *Perotis rara* were consistently preferred, while others such as *A. contorta*, *T. basedowii* and Goodeniaceae were avoided.

In Tables 4.4, 4.5, 4.6, and 4.7, similar analyses are presented separately for each rodent population phase and for the seed crop on plants and in the seed bank. It is worth noting that, not only did the diet change during phases, but so too did the preference for certain seed species. The two rodent species appeared to show consistently similar patterns of selection or avoidance for some seed species (e.g. *A. contorta*, *T. basedowii*, *Sida* sp., *Euphorbia* sp., *C. balonensis*) but different patterns for others (e.g. *T. glaucifolia*, *G. cycloptera*, *E. aristidea*) during the different population phases.

4.3.2.6. Contribution of different food categories to diets of the two rodent species during different phases: SIMPER analyses

SIMPER comparison of the diet of *P. hermannsburgensis* between population phases are presented in Table 4.8. A cut-off of a cumulative percentage dissimilarity of 80 % was applied. The food categories that contributed most to differences in phases were Invertebrates, *Trachymene glaucifolia*, *Triodia basedowii*, and *Ptilotus polystachyus*. *Pseudomys hermannsburgensis* consumed a large amount of Invertebrates and seed of *T. basedowii* during the High population phase. *Trachymene glaucifolia* seed was eaten most during the Decreasing phase, and *P. polystachyus* seed mostly during the Low phase. ANOSIM on diet with the phases as factors was significant (Global R=0.271, P=0.001). The 2-d stress in the MDS analysis of the separation between phases was 0.18, and this allowed clear interpretation of the ordination (Fig. 4.12).

Table 4.2. Comparison of the overall seed species and families identified in the gut contents of *N. alexis* with availability of the same taxa in plant survey and soil samples. In columns two and four are the rankings for each seed species from the least preferred (1) to the most preferred (36). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

Species	Gut contents vs plant survey	Species	Gut contents vs soil sample
Amaranthaceae	1	Goodeniaceae	1
G. stenobotrya	2	*G. stenobotrya*	2
Goodeniaceae	3	Fabaceae	3
A. contorta	4	*T. basedowii*	4.5
T. basedowii	5.5	*P. refractum*	4.5
E. drummondii	5.5	*A. contorta*	6
C. balonensis	7	Amaranthaceae	7
Fabaceae	8	*S. fibulifera*	8.5
D. radulans	9	*E. drummondii*	8.5
E. tannensis	10	*D. radulans*	10
Scaveola sp.	11.5	*O. pterospora*	11
P. refractum	11.5	*T. glaucifolia*	12
T. glaucifolia	13.5	*G. cycloptera*	13
O. pterospora	13.5	Chenopodiaceae	14
E. aristidea	15	*Tribulus* sp.	15
G. cycloptera	16	*E. aristidea*	16
S. fibulifera	17	*D. viscosa*	17
P. polystachyus	18	*E. eriopoda*	18
Euphorbia sp.	19	*C. balonensis*	19
T. pilosa	20	*E. tannensis*	20
Poaceae other	21	*T. pilosa*	21
E. eriopoda	22	*Eucalyptus* sp.	22.5
P. intraterranea	23	*Grevillea* sp.	22.5
G. juncifolia	24	*P. rara*	24
Sida sp.	25	Poaceae other	25
E. macdonnelli	26	*Cassia* sp.	26.5
Chenopodiaceae	27	*G. juncifolia*	26.5
Cassia sp.	28	*Scaveola* sp.	28
S. bicornis	29	*P. intraterranea*	29
D. viscosa	30	*Crotalaria* sp.	30
Crotalaria sp.	31	*E. macdonnelli*	31
Tribulus sp.	33	*Euphorbia* sp.	32
Eucalyptus sp.	33	*S. bicornis*	33
Grevillea sp.	33	*E. tomentosa*	34
P. rara	35	*P. polystachyus*	35
E. tomentosa	36	*Sida* sp.	36

Table 4.3. Comparison of the overall seed species and families identified in the gut contents of *P. hermannsburgensis* with availability of the same taxa in plant survey and soil samples. In columns two and four are the rankings for each seed species from the least preferred (1) to the most preferred (36). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

Species	**Gut contents vs plant survey**	**Species**	**Gut contents vs soil sample**
A. contorta	1	*C. erinacaea*	1
G. cycloptera	2.5	Fabaceae	2
Y. australiensis	2.5	*G. cycloptera*	3
Fabaceae	4	*A. contorta*	4
E. tannensis	5.5	*D. viscosa*	5
T. basedowii	5.5	*Y. australiensis*	6
E. aristidea	7	*C. artemisioides*	7
C. balonensis	8	*T. basedowii*	8.5
T. glaucifolia	9	Chenopodiaceae	8.5
D. radulans	10	*E. tannensis*	10
Euphorbia sp.	11.5	*E. eriopoda*	11
Poaceae other	11.5	*E. aristidea*	12
T. pilosa	13.5	*T. glaucifolia*	13.5
P. polystachyus	13.5	*T. pilosa*	13.5
T. australianus	15	*D. radulans*	15
C. erinacaea	16	Poaceae other	16
A. dictyophleba	17	*C. balonensis*	17
Sida sp.	18	Malvaceae	18
Eremophila sp.	19.5	*A. dictyophleba*	20
E. eriopoda	19.5	*Eucalyptus* sp.	20
Malvaceae	21	*T. australianus*	20
Chenopodiaceae	22	*Eremophila* sp.	22
D .viscosa	23	*Atriplex* sp.	23
S. bicornis	24	*Euphorbia* sp.	24
Eucalyptus sp.	25	Portulacaceae	25
C. artemisioides	26	*P. rara*	26
Atriplex sp.	27	*Sida* sp.	27
Portulacaceae	28	*S. bicornis*	28
P. rara	29	*Grevillea* sp.	29
Grevillea sp.	30	*P. polystachyus*	30

Table 4.4. Comparison of seed species and family identified in the gut contents of *N. alexis* with availability of the same taxa in the plant survey. Columns two, four, six, and eight show the rankings for each seed species from the least preferred (1) to the most preferred (n). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

High phase	Ranks	**Decreasing phase**	Ranks	**Low phase**	Ranks	**Increasing phase**	Ranks
A. contorta	1	*C. balonensis*	1	*T. basedowii*	1	*T. basedowii*	1
E. drummondii	2	*A. contorta*	2	Goodeniaceae	2	Amaranthaceae	2.5
E. aristidea	3	*D. radulans*	3	*A. contorta*	3	*E. drummondii*	2.5
E. tannensis	4.5	*G. stenobotrya*	4	*C. balonensis*	4	*G. stenobotrya*	4
T. basedowii	4.5	*E. drummondii*	5	*G. cycloptera*	5.5	*A. contorta*	5
O. pterospora	6	*E. eriopoda*	6	*P. polystachyus*	5.5	*P. refractum*	6
P. refractum	7	*P. intraterranea*	7	*E. aristidea*	7.5	*G. cycloptera*	7
G. cycloptera	8	*O. pterospora*	8.5	Poaceae	7.5	*E. tannensis*	8.5
Sida sp.	9	*T. basedowii*	8.5	*P. refractum*	9	*T. glaucifolia*	8.5
D. radulans	10	*E. aristidea*	10.5	*P. intraterranea*	10	Goodeniaceae	10
D. viscosa	11	*G. cycloptera*	10.5	*E. tannensis*	11	*E. aristidea*	11
Chenopodiaceae	12	*C. cunninghamii*	12	*Sida* sp.	12	*C. balonensis*	12
C. balonensis	13	*E. tannensis*	13	*D. radulans*	13	*D. radulans*	13
Tribulus sp.	14	*T. glaucifolia*	14	*Cassia* sp.	14	Poaceae	14
Euphorbia sp.	15	Poaceae	15.5	*S. bicornis*	15	*O. pterospora*	15
T. pilosa	16	*P. polystachyus*	15.5			*P. intraterranea*	16
T. glaucifolia	17	*Sida* sp.	17			*P. polystachyus*	17
		Chenopodiaceae	18			*T. pilosa*	18
		Cassia sp.	19.5			Fabaceae	19
		Euphorbia sp.	19.5			*S. fibulifera*	20
		G. juncifolia	21			Chenopodiaceae	21
		D. viscosa	22			*C. cunninghamii*	22
		Scaveola sp.	23			*Eucalyptus* sp.	23
		E. tomentosa	24			*P. rara*	24
						Sida sp.	25
						S. bicornis	26
						E. macdonnelli	27
						E. tomentosa	28

Table 4.5. Comparison of seed species and family identified in the gut contents of *P. hermannsburgensis* with availability of the same taxa in the plant survey. Columns two, four, six, and eight show the rankings for each seed species from the least preferred (1) to the most preferred (n). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

High phase	Ranks	**Decreasing phase**	Ranks	**Low phase**	Ranks	**Increasing phase**	Ranks
G. cycloptera	1	*A. contorta*	1	*A. contorta*	1	*T. basedowii*	1
Fabaceae	2	*E. tannensis*	2	*T. basedowii*	2	*Y. australiensis*	2
A. contorta	3	*C. balonensis*	3.5	Poaceae	3.5	*E. aristidea*	3.5
C. balonensis	4	*G. stenobotrya*	3.5	*T. glaucifolia*	3.5	*E. tannensis*	3.5
E. aristidea	5.5	Poaceae	5	*E. aristidea*	5	*D. radulans*	5
T. basedowii	5.5	*G. cycloptera*	6	*G. cycloptera*	6	*C. balonensis*	6
G. stenobotrya	7	*P. polystachyus*	7	*C. balonensis*	7	*T. glaucifolia*	7
Poaceae	8	*A. dictyophleba*	8	*P. polystachyus*	8	*G. stenobotrya*	8
T. glaucifolia	9	*T. glaucifolia*	9	*Sida* sp.	9	Poaceae	9
E. tannensis	10	*E. eriopoda*	10	*E. tannensis*	10	*Sida* sp.	10
Sida sp.	11	*D. viscosa*	11	*C. erinacaea*	11	Chenopodiaceae	11
Chenopodiaceae	12	*T. australianus*	12	Chenopodiaceae	12	*S. bicornis*	12
A. nummilaria	13.5	*Cassia* sp.	13.5	*Euphorbia* sp.	13	*P. rara*	13
D. radulans	13.5	Chenopodiaceae	13.5	*Eucalyptus* sp.	14.5	Portulacaceae	14
Euphorbia sp.	15	*D. radulans*	15	Malvaceae	14.5		
Portulacaceae	16	Portulacaceae	16	*Eremophila* sp.	16		
P. rara	17	*Sida* sp.	17	Portulacaceae	17		
T. pilosa	18	*P. rara*	18				

Table 4.6. Comparison of seed species and family identified in the gut contents of *N. alexis* with availability of the same taxa in the soil samples. Columns two, four, six, and eight show the rankings for each seed species from the least preferred (1) to the most preferred (n). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

High phase	Ranks	**Decreasing phase**	Ranks	**Low phase**	Ranks	**Increasing phase**	Ranks
P. refractum	1	*A. contorta*	1	*T. basedowii*	1	*T. basedowii*	1
A. contorta	2	*O. pterospora*	2.5	*G. cycloptera*	2	*G. stenobotrya*	2.5
E. tannensis	3	*E. drummondii*	2.5	*A. contorta*	3	*P. refractum*	2.5
T. basedowii	4	*G. stenobotrya*	4	Chenopodiaceae	4	*G. cycloptera*	4
E. drummondii	5	*S. fibulifera*	5.5	*D. radulans*	5	Amaranthaceae	6.5
Poaceae	6.5	*T. basedowii*	5.5	*P. refractum*	6	*O. pterospora*	6.5
E. aristidea	6.5	*S. parvifolia*	7	*E. aristidea*	7	*P. intraterranea*	6.5
Chenopodiaceae	8	*T. glaucifolia*	8	Poaceae	8	*T. glaucifolia*	6.5
T. glaucifolia	9	*E. aristidea*	9	*Sclerolaena* sp.	9	Fabaceae	9
D. radulans	10	*C. balonensis*	12.5	*C. balonensis*	10	*E. drummondii*	11
G. cycloptera	11	*Cassia* sp.	12.5	*E. tannensis*	11	*Eucalyptus* sp.	11
D. viscosa	12	*E. eriopoda*	12.5	Goodeniaceae	12	Goodeniaceae	11
O. pterospora	13	*Euphorbia* sp.	12.5	*Cassia* sp.	13	*P. rara*	13
C. balonensis	14	*P. intraterranea*	12.5	*Sida* sp.	14	*E. aristidea*	14
Tribulus sp.	15	Poaceae	12.5	*P. polystachyus*	15	*E. tannensis*	15
Euphorbia sp.	16	*G. cycloptera*	16	*P. intraterranea*	16	*S. fibulifera*	16
T. pilosa	17	*C. cunninghamii*	17.5			*A. contorta*	18
Sida sp.	18	*D. radulans*	17.5			*P. polystachyus*	18
		G. juncifolia	19			*T. pilosa*	18
		E. tannensis	20			*C. cunninghamii*	20
		D. viscosa	21			*Sclerolaena* sp.	21
		E. tomentosa	22			*D. radulans*	22
		Chenopodiaceae	23			Chenopodiaceae	23
		P. polystachyus	24			*E. macdonellii*	24
						C. balonensis	25
						E. tomentosa	26
						Poaceae	27
						Sida sp.	28

Table 4.7. Comparison of seed species and family identified in the gut contents of *P. hermannsburgensis* with availability of the same taxa in the soil samples. Columns two, four, six, and eight show the rankings for each seed species from the least preferred (1) to the most preferred (n). Analysis modified from Johnson (1980). Full names of plant species are given in Appendix 3 (Table 1).

High phase	Ranks	**Decreasing phase**	Ranks	**Low phase**	Ranks	**Increasing phase**	Ranks
G. cycloptera	1	*A. contorta*	1	*A. contorta*	1	*T. basedowii*	1
Chenopodiaceae	2	*G. cycloptera*	2	*T. basedowii*	2	Chenopodiaceae	2.5
Poaceae	3	Poaceae	3	*C. erinacaea*	3	*T. glaucifolia*	2.5
A. contorta	4.5	*T. glaucifolia*	4	*G. cycloptera*	4	*D. radulans*	4
T. glaucifolia	4.5	Portulacaceae	5	*T. glaucifolia*	5	*E. aristidea*	5
Fabaceae	6	*G. stenobotrya*	6	Poaceae	6	Poaceae	6.5
E. aristidea	7.5	*E. tannensis*	7	*E. aristidea*	7	*Y. australiensis*	6.5
T. basedowii	7.5	*D. viscosa*	8	Chenopodiaceae	8	*G. stenobotrya*	8
E. tannensis	9	*A. dictyophleba*	9.5	*C. balonensis*	9	*E. tannensis*	9
G. stenobotrya	10	*T. australianus*	9.5	Malvaceae	10	*Sida* sp.	10
D. radulans	11	*C. artemisioides*	11	*E. tannensis*	11	*P. rara*	11
Atriplex sp.	12.5	Chenopodiaceae	12	*Eucalyptus* sp.	12	Portulacaceae	12
Euphorbia sp.	12.5	*Sida* sp.	13	*Eremophila* sp.	13	*Sclerolaena* sp.	13
Portulacaceae	14	*E. eriopoda*	14	Portulacaceae	14	*C. balonensis*	14
P. rara	15	*C. balonensis*	15	*Euphorbia* sp.	15		
Sida sp.	16	*P. rara*	16	*Sida* sp.	16		
C. balonensis	17	*P. polystachyus*	17	*P. polystachyus*	17		
T. pilosa	18	*D. radulans*	18				

Table 4.8. Results of similarity terms (SIMPER) analysis on gut contents of *P. hermannsburgensis* in four phases of the population cycle. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of food type in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	Av.Abund	Av.Abund	Av.Diss	Contrib%
	Phase D	**Phase H**		
Invertebrates	9.30	50.14	27.97	32.03
T. glaucifolia	33.66	1.48	20.31	23.25
T. basedowii	0.00	13.31	8.85	10.13
D. radulans	7.53	0.77	4.66	5.33
E. aristidea	0.00	7.25	4.40	5.04
Grevillea sp.	0.00	5.49	3.33	3.81
	Phase D	**Phase I**		
T. glaucifolia	33.66	8.31	24.39	29.12
Invertebrates	9.30	28.66	18.91	22.58
D. radulans	7.53	1.41	5.46	6.52
Grass material	0.70	7.60	4.97	5.93
C. balonensis	1.27	5.99	4.54	5.42
S. bicornis	0.00	6.13	4.12	4.92
Chenopodiaceae	2.39	5.21	3.53	4.21
	Phase H	**Phase I**		
Invertebrates	50.14	28.66	24.83	33.41
T. basedowii	13.31	1.83	8.59	11.56
T. glaucifolia	1.48	8.31	5.17	6.95
E. aristidea	7.25	1.69	4.64	6.24
C. balonensis	1.55	5.99	4.15	5.59
Grass material	0.00	7.60	4.14	5.57
S. bicornis	0.00	6.13	3.62	4.87
Chenopodiaceae	0.28	5.21	3.34	4.49
	Phase D	**Phase L**		
T. glaucifolia	33.66	3.87	22.64	26.66
Invertebrates	9.30	25.84	17.35	20.43
P. polystachyus	3.66	21.83	14.94	17.59
D. radulans	7.53	0.00	5.26	6.20
C. balonensis	1.27	6.34	4.69	5.52
	Phase H	**Phase L**		
Invertebrates	50.14	25.84	27.07	34.76
P. polystachyus	0.00	21.83	12.22	15.69
T. basedowii	13.31	1.13	8.84	11.35
E. aristidea	7.25	1.97	4.92	6.32
C. balonensis	1.55	6.34	4.24	5.44
Grevillea sp.	5.49	0.00	3.33	4.28
	Phase I	**Phase L**		
Invertebrates	28.66	25.84	22.68	27.72
P. polystachyus	0.00	21.83	13.31	16.28
T. glaucifolia	8.31	3.87	7.05	8.62
C. balonensis	5.99	6.34	7.03	8.59
Grass material	7.60	1.62	5.52	6.75
Chenopodiaceae	5.21	3.38	5.01	6.13
S. bicornis	6.13	0.00	4.15	5.08

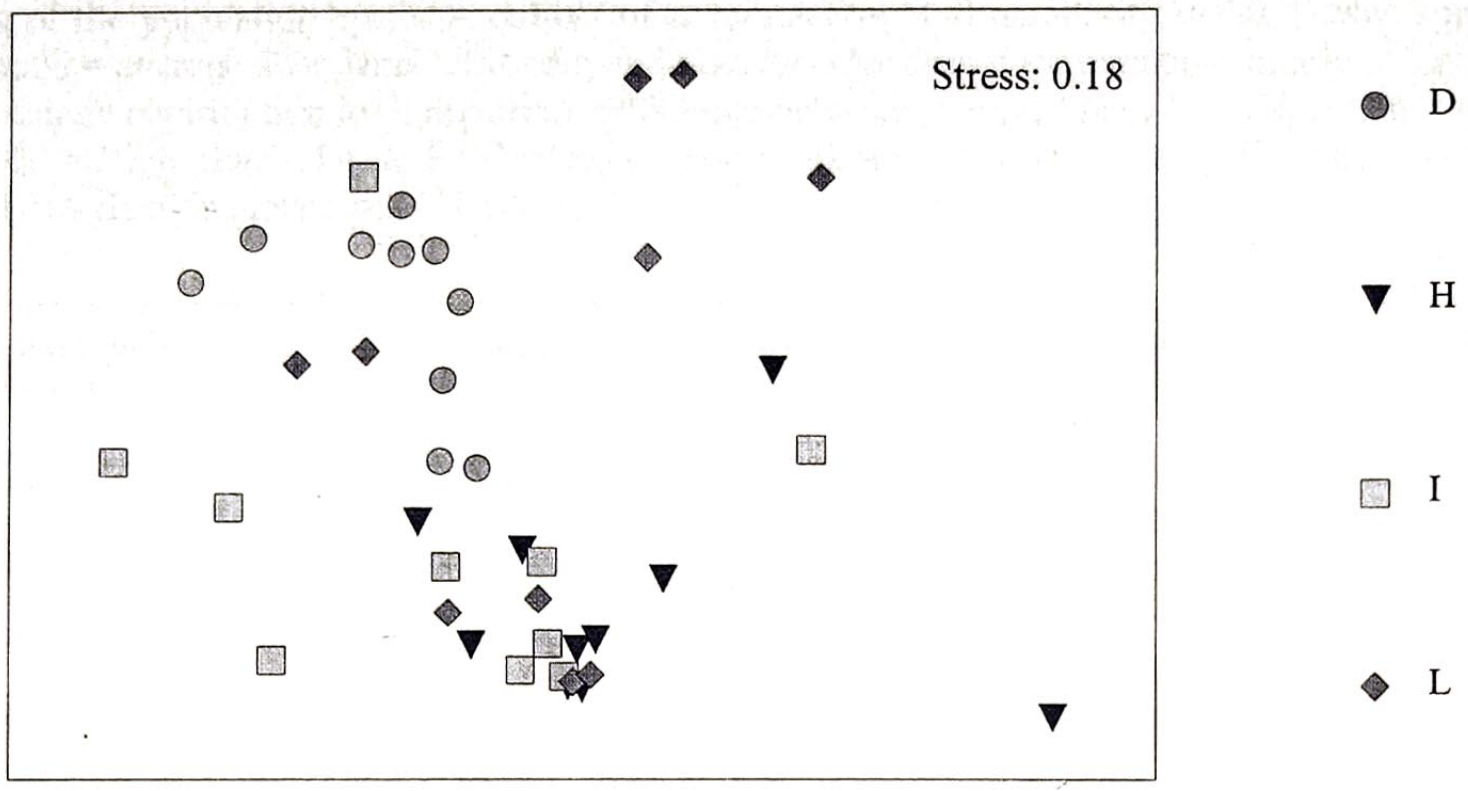


Figure 4.12. MDS of species-level categories of food items in the diet of *P. hermannsburgensis* during different population phases. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

The pairwise tests between phases showed that all the phases differed significantly from each other, with the exception of Increasing and Low (Table 4.9).

Table 4.9. Pairwise ANOSIM tests on the gut contents of *P. hermannsburgensis* between population phases. H, high phase, D, decreasing phase, L, low phase, and I, increasing phase.

Phase comparison	***R***	***P***
D vs H	0.667	0.001
D vs I	0.424	0.001
D vs L	0.332	0.002
H vs I	0.114	0.031
H vs L	0.125	0.035
I vs L	0.068	0.147

Table 4.10 shows the results of SIMPER analysis performed on species-level items of food in the gut of *N. alexis*. A cut-off of a cumulative percentage dissimilarity of 80 % was again applied. The main differences between population phases were due to Fruit A, *T. glaucifolia* seed, Invertebrates, seed from *Sida* sp., and Chenopodiaceae. Fruit A was consumed mainly during the High population phase, and *T. glaucifolia* seed mainly during the Decreasing phase. *Notomys alexis* ate a large quantity of Invertebrates during the

Table 4.10. Results of similarity terms (SIMPER) analysis on gut contents of *N. alexis* in four phases of the population cycle. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of food type in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase D	**Phase H**		
Fruit A	0.00	17.04	10.53	12.78
T. glaucifolia	13.64	8.03	8.79	10.66
Invertebrates	10.12	8.86	6.53	7.93
G. cycloptera	2.07	7.12	4.77	5.79
E. aristidea	3.24	6.36	4.37	5.30
Chenopodiaceae	7.02	1.97	4.22	5.11
Floral parts	0.55	6.36	4.09	4.96
Seed G	6.27	0.38	3.59	4.35
Plant material	0.00	5.76	3.44	4.18
Sida sp.	2.48	5.68	3.42	4.15
T. basedowii	3.79	2.42	3.03	3.67
Poaceae	5.03	0.98	2.89	3.51
Yellow husk	0.00	4.70	2.87	3.49
	Phase D	**Phase I**		
Invertebrates	10.12	29.48	17.00	20.32
T. glaucifolia	13.64	1.26	9.23	11.04
Chenopodiaceae	7.02	8.27	6.48	7.75
Poaceae	5.03	5.74	5.44	6.50
Sida sp.	2.48	7.45	5.42	6.48
S. fibulifera	0.00	5.81	4.08	4.88
E. tomentosa	1.17	4.86	3.96	4.74
Seed G	6.27	0.00	3.51	4.19
Plant material	0.00	4.23	2.77	3.31
E. aristidea	3.24	1.39	2.31	2.77
T. basedowii	3.79	0.13	2.28	2.72
	Phase H	**Phase I**		
Invertebrates	8.86	29.48	15.14	17.48
Fruit A	17.04	0.00	9.80	11.32
Sida sp.	5.68	7.45	5.81	6.71
Chenopodiaceae	1.97	8.27	5.04	5.82
Plant material	5.76	4.23	4.95	5.72
T. glaucifolia	8.03	1.26	4.90	5.66
G. cycloptera	7.12	0.63	4.09	4.73
Floral parts	6.36	0.00	3.65	4.22
E. aristidea	6.36	1.39	3.61	4.17
Poaceae	0.98	5.74	3.59	4.15
S. fibulifera	0.00	5.81	3.58	4.13
E. tomentosa	0.00	4.86	2.99	3.45
	Phase D	**Phase L**		
Invertebrates	10.12	36.74	19.42	23.80
Chenopodiaceae	7.02	20.76	11.43	14.01
T. glaucifolia	13.64	0.00	8.63	10.57
P. intraterranea	0.07	9.70	5.74	7.03
P. polystachyus	2.89	6.36	5.41	6.63

continue

Table 4.10. continued

Food categories	Av.Abund	Av.Abund	Av.Diss	Contrib%
E. aristidea	3.24	6.74	4.65	5.70
Seed G	6.27	0.00	3.27	4.01
Poaceae	5.03	3.94	3.18	3.90
	Phase H	**Phase L**		
Invertebrates	8.86	36.74	17.54	20.21
Chenopodiaceae	1.97	20.76	10.87	12.53
Fruit A	17.04	0.00	9.12	10.52
P. intraterranea	0.00	9.70	5.14	5.92
E. aristidea	6.36	6.74	4.69	5.40
T. glaucifolia	8.03	0.00	4.45	5.13
G. cycloptera	7.12	0.61	3.83	4.42
Floral parts	6.36	0.46	3.53	4.06
P. polystachyus	0.00	6.36	3.50	4.04
Sida sp.	5.68	0.68	3.04	3.50
Plant material	5.76	0.00	3.00	3.46
	Phase I	**Phase L**		
Invertebrates	29.48	36.74	18.57	25.42
Chenopodiaceae	8.27	20.76	10.78	14.76
P. intraterranea	0.06	9.70	5.36	7.34
Sida sp.	7.45	0.68	4.42	6.05
Poaceae	5.74	3.94	4.30	5.89
E. aristidea	1.39	6.74	3.96	5.42
P. polystachyus	0.63	6.36	3.89	5.32
S. fibulifera	5.81	0.00	3.46	4.73
E. tomentosa	4.86	0.00	2.89	3.95

Increasing and Low phases. *Sida* sp. seed was consumed mostly during Increasing and High phases and Chenopodiaceae during Low and Increasing phases. The separation between phases in the MDS analysis was less clear than for *P. hermannsburgensis*, and was associated with a high stress of 0.23 (Fig. 4.13).

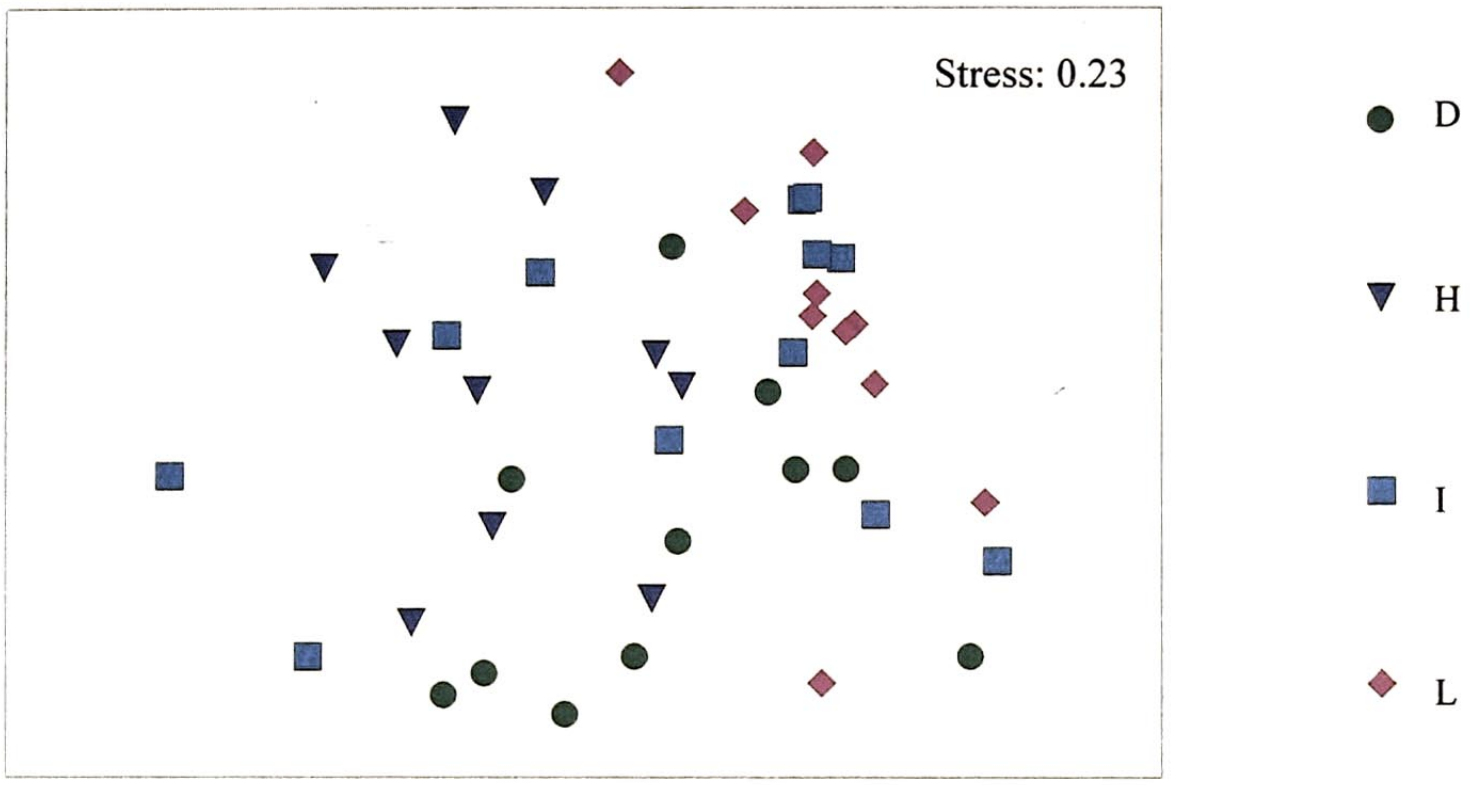


Figure 4.13. MDS of species-level categories of food items in the diet of *N. alexis* during different population phases. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

The ANOSIM on diet with the population phases as factors was significant (Global R=0.217, P=0.001). Pairwise tests between phases showed no difference between Increasing and Low phases (Table 4.11), although other comparisons were significant.

Table 4.11. Pairwise ANOSIM tests on the gut contents of *N. alexis* between population phases. H, high phase, D, decreasing phase, L, low phase, and I, increasing phase.

Phase comparison	***R***	***P***
D vs H	0. 202	0.014
D vs I	0.132	0.033
D vs L	0.322	0.004
H vs I	0.254	0.003
H vs L	0.508	0.001
I vs L	0.003	0.390

4.3.2.7. Comparison of the diets of the two rodent species: SIMPER analyses

Pseudomys hermannsburgensis consumed more Invertebrates, Plant material, seeds of *Trachymene glaucifolia*, *Ptilotus polystachyus*, *Triodia basedowii*, *Calandrinia balonensis*, Grass material and *Dactyloctenium radulans* seed than *N. alexis*, which consumed more seeds of Chenopodiaceae, *Eriachne aristidea*, Poaceae, *Sida* sp., and Fruit A (Table 4.12).

Table 4.12. Results of similarity terms (SIMPER) analysis on the gut contents of the two rodent species. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of food type in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	P. hermann.	***N. alexis***		
Invertebrates	28.52	21.42	15.31	21.01
*Plant material	22.16	20.90	9.82	13.47
T. glaucifolia	11.83	5.71	7.04	9.66
Chenopodiaceae	2.82	9.39	4.88	6.70
P. polystachyus	6.37	2.40	4.10	5.63
E. aristidea	2.73	4.26	2.96	4.06
T. basedowii	4.07	1.60	2.56	3.51
C. balonensis	3.78	1.32	2.42	3.33
Poaceae	2.01	4.03	2.42	3.32
Sida sp.	1.46	4.19	2.35	3.22
Fruit A	0.05	3.96	2.00	2.75
*Grass material	2.48	0.78	1.56	2.14
D. radulans	2.43	0.48	1.38	1.90

* the two categories have been combined in Figure 4.6

In the analysis of gross food categories, *P. hermannsburgensis* consumed more Invertebrates and seeds of Poaceae, Apiaceae and Amaranthaceae than *N. alexis*, which ate more Chenopodiaceae seed (Table 4.13).

Table 4.13. Results of similarity terms (SIMPER) analysis on the gut contents of the two rodent species, dividing seeds into family categories. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of food type in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups.

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	P. hermann.	***N. alexis***		
Invertebrates	28.52	21.42	21.01	28.14
Poaceae	13.34	11.26	11.39	15.25
Apiaceae	11.83	5.71	10.41	13.94
Chenopodiaceae	4.44	11.93	8.45	11.32
Amaranthaceae	6.37	2.41	5.48	7.35

With regards to plant type, *P. hermannsburgensis* consumed more Forb and Grass seed than *N. alexis* (Table 4.14).

Table 4.14. Results of similarity terms (SIMPER) analysis on the gut contents of the two rodent species, dividing seeds into type categories. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of food type in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups.

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	P. hermann.	***N. alexis***		
Invertebrates	28.52	21.42	19.68	29.78
Forbs	23.77	18.75	17.74	26.85
Grasses	15.83	12.03	11.48	17.37

The ANOSIM on food eaten at the seed species level by the two rodent species was significant (Global R=0.042, P=0.017), as was the ANOSIM on plant family and food type categories eaten (Global R=0.054, P=0.011, and Global R=0.06, P=0.007, respectively). No significant difference was found between the rodent species with respect to ingestion of seeds in the annual/perennial plant categories (Global R=0.028, P=0.065).

4.3.2.8. Are there differences in diet between different reproductive categories of rodents?

Pregnant female *N. alexis* consumed significantly more 'animal remains' (U=67.50, P=0.034) and seed from *Euphorbia* sp. (U=67.50, P=0.034) than did other adults of this

species. The category 'animal remains' does not include invertebrates and because of its very low abundance in the rodent diets was not presented in the previous analyses and graphical representations for categories of abundance > 0.5% When gross categories were considered for the same species the only significant result was that adult *N. alexis* consumed more seed from Portulacaceae (U=45.00, P=0.025) than pregnant females. In *P. hermannsburgensis*, pregnant females ate more *E. tannensis* seed (U=28.00, P=0.027) than other adults. If gross categories are considered, pregnant females consumed more seed from Euphorbiaceae (U=28.00, P=0.027) than other adults.

From the SIMPER analysis for *P. hermannsburgensis*, no difference was observed in diet between sexes (Global R=-0.009, P=0.526) or between individuals in different reproductive condition (Global R=0.099, P=0.128). The same pattern was observed for *N. alexis* in the SIMPER analysis for sexes (Global R=-0.052, P=0.991) and reproductive condition (Global R=0.033, P=0.257).

4.3.2.9. How different are the diets of the two rodent species during different population phases? Niche breadth and overlap

The breadths and overlaps in diet of the two study species in the four population phases are presented in Table 4.15.

Table 4.15. Niche breadth and overlap of the diet of the two study species in the four population phases analysed. Two indices of niche overlap are considered, Pianka's index and Renkonen's index. The diet was analysed by partitioning foods into gross categories (Seeds, Plant material, Invertebrates, Fruits, and Other), and fine categories. H, high phase, D, decreasing phase, L, low phase, and I, increasing phase.

Phases	**Niche breadth**		**Niche overlap**			
	N. alexis	***P. hermann.***	**Pianka's index Gross categories**	**Renkonen's index (%) Gross categories**	**Pianka's index Fine categories**	**Renkonen's index (%) Fine categories**
H	12.511	3.464	0.659	58.029	0.433	35.402
D	8.321	4.530	0.997	95.052	0.862	61.395
L	4.944	5.416	0.926	78.151	0.686	48.087
I	7.048	6.144	0.984	91.909	0.898	64.245

It is interesting to observe that during the High and Decreasing phases *N. alexis* had a much larger dietary niche breadth than *P. hermannsburgensis*, and appeared to be a more generalist forager than *P. hermannsburgensis*. However, during the Low and Increasing phases the niche breadths of the two species became similar, and tended toward specialist consumption in the Low phase. Maximal overlap in the diets of the two species was observed during the Decreasing and Increasing phases, while smaller overlap occurred during the High and then Low phases. The two overlap indices provided slightly different results, especially with regard to the gross analysis during the Low phase, but showed the same pattern between phases. In addition, when fine categories are considered the overlaps between species decreased in each phase.

Notomys alexis tended to eat a greater variety of food items than *P. hermannsburgensis* during each population phase (Table 4.16), although a chi-square test on numbers of food items ingested was not significant (χ^2= 1.99, df=3, P>0.05).

Table 4.16. Number of food items in the diet of the two species during different population phases.

Phases	**Number of food items in the diet**	
	N. alexis	***P. hermannsburgensis***
High	32	26
Decreasing	37	26
Low	24	24
Increasing	36	21

4.3.3. Does rainfall influence changes in plant cover, and does plant cover influence changes in rodent numbers (Model 2)?

Correlations of average monthly plant cover and plant cover species diversity with the modified cumulative monthly rainfall residual (CDMR) and with the capture rates per trap-night of the two rodent species at Ethabuka site (first and second predictions of Model 2) are presented in Appendices 4 to 9 (Tables 2-7). Plant cover and plant cover species diversity were correlated significantly with rainfall with time lags of four-six months and one month, respectively. *Notomys alexis* capture rates were correlated significantly with the average monthly cover at T_0 (no time lag), at T_3 (3-month lag) and at T_7 (7-month lag), but the highest correlation coefficient was at T_3. A significant correlation was found between *N. alexis* capture rates and species diversity of plant cover with a time lag of five

months. *Pseudomys hermannsburgensis* capture rates were correlated significantly with the plant cover without any time lag (T_0), and with species diversity of plant cover with a time lag of five months.

4.3.4. Does rainfall influence changes in food resources, which in turn trigger changes in rodent numbers (Model 3)?

The modified monthly CDMR was correlated with the monthly seed crop index, the monthly flower crop index, the monthly seed abundance in the seed bank (first prediction of Model 3), and the species diversity for each of these categories (results presented in Appendices 10 to 13 - Tables 8-11). The results for the soil samples are not presented because correlations were not significant for any time lag (*r*-values ranged from –0.384 to 0.157 for the monthly seed abundance, and from –0.172 to 0.251 for species diversity, $P>0.05$). Resource abundances were generally correlated significantly with rainfall in the first two months after rain. Species diversity of seed and flower crops was also correlated with rain in the first two months. The second prediction of Model 3 was tested by correlating capture rates per trap-night of the two species with the seed crop index, the flower crop index, seed abundance in the seed bank and the species diversity of each of these food categories. Correlations with plant cover and plant cover species diversity were performed for Model 2, above. Only significant correlations are presented (Appendices 14 and 15 - Tables 12 and 13). *Notomys* alexis capture rates were not correlated with any of the three indices of food resources or their species diversity. However, a significant correlation was found between *P. hermannsburgensis* capture rates and the monthly seed crop index with a time lag of three months. In the case of the monthly flower crop index, the only time lag producing a significant correlation was nine months. There were no significant correlations between *P. hermannsburgensis* capture rates and monthly seed abundances from soil samples, or with species diversity of each food resource.

4.3.4.1. Food resource changes during population cycles of the two rodent species: SIMPER analyses

The results of the multivariate analyses comparing the differences in plant cover between population phases of *N. alexis* and *P. hermannsburgensis* (prediction 3 of Model 3, diet should change with changes in food resources) are reported in Table 4.17. The main categories that contributed to differences in phases were *T. basedowii*, *A. contorta*, *E.*

Table 4.17. Results of similarity terms (SIMPER) analysis on plant cover in the four population phases of the two species of study rodents. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of species in the diet, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase D	**Phase H**		
T. basedowii	26.92	37.99	15.67	38.05
A. contorta	1.90	8.20	6.10	14.82
E. aristidea	0.49	2.93	2.38	5.77
G. stenobotrya	2.89	5.02	2.16	5.25
E. drummondii	0.56	1.71	1.30	3.15
S. parvifolia	0.37	0.62	0.93	2.26
S. fibulifera	0.51	0.45	0.82	1.99
C. balonensis	0.42	0.40	0.63	1.54
Sida sp.	0.25	0.81	0.60	1.46
A. ligulata	0.39	0.72	0.56	1.36
G. juncifolia	0.15	0.57	0.54	1.31
C. eremaea	0.14	0.66	0.52	1.26
E. longifolia	0.28	0.58	0.51	1.24
	Phase D	**Phase I**		
T. basedowii	26.92	26.51	16.13	41.27
A. contorta	1.90	2.57	2.73	6.98
G. stenobotrya	2.89	3.86	1.73	4.42
T. glaucifolia	0.27	1.30	1.48	3.78
E. drummondii	0.56	1.25	1.41	3.62
C. balonensis	0.42	1.32	1.35	3.47
S. fibulifera	0.51	0.74	1.02	2.62
E. aristidea	0.49	0.75	0.96	2.46
S. parvifolia	0.37	0.56	0.85	2.17
E. longifolia	0.28	0.68	0.67	1.72
G. cycloptera	0.21	0.59	0.66	1.68
A. ligulata	0.39	0.68	0.65	1.67
Y. australiensis	0.27	0.44	0.62	1.60
A. dictyophleba	0.33	0.43	0.50	1.29
	Phase H	**Phase I**		
T. basedowii	37.99	26.51	12.32	33.26
A. contorta	8.20	2.57	4.87	13.16
E. aristidea	2.93	0.75	1.91	5.16
G. stenobotrya	5.02	3.86	1.34	3.61
T. glaucifolia	0.14	1.30	1.07	2.89
C. balonensis	0.40	1.32	1.07	2.89
E. drummondii	1.71	1.25	0.97	2.61
S. parvifolia	0.62	0.56	0.95	2.57
S. fibulifera	0.45	0.74	0.88	2.38
E. longifolia	0.58	0.68	0.67	1.81
Sida sp.	0.81	0.35	0.51	1.39
G. cycloptera	0.59	0.59	0.47	1.27
G. juncifolia	0.57	0.04	0.46	1.25
A. ligulata	0.72	0.68	0.45	1.22

continue

Table 4.17. continued

Food categories	Av.Abund	Av.Abund	Av.Diss	Contrib%
S. spinescens	0.41	0.29	0.45	1.21
T. rosea	0.52	0.39	0.44	1.18
Y. australiensis	0.36	0.44	0.43	1.17
	Phase D	**Phase L**		
T. basedowii	26.92	24.83	19.46	51.49
A. contorta	1.90	1.46	2.24	5.92
G. stenobotrya	2.89	2.70	1.42	3.76
S. parvifolia	0.37	0.94	1.12	2.98
S. fibulifera	0.51	0.80	0.96	2.53
T. glaucifolia	0.27	0.46	0.81	2.14
E. drummondii	0.56	0.20	0.78	2.07
C. balonensis	0.42	0.43	0.78	2.07
E. aristidea	0.49	0.16	0.65	1.71
A. ligulata	0.39	0.44	0.61	1.62
T. rosea	0.28	0.44	0.49	1.28
P. polystachyus	0.21	0.22	0.48	1.27
A. dictyophleba	0.33	0.14	0.43	1.13
	Phase H	**Phase L**		
T. basedowii	37.99	24.83	14.71	34.36
A. contorta	8.20	1.46	6.45	15.07
E. aristidea	2.93	0.16	2.63	6.15
G. stenobotrya	5.02	2.70	2.33	5.45
E. drummondii	1.71	0.20	1.48	3.45
S. parvifolia	0.62	0.94	1.30	3.03
S. fibulifera	0.45	0.80	0.99	2.32
Sida sp.	0.81	0.16	0.67	1.56
C. balonensis	0.40	0.43	0.64	1.50
E. longifolia	0.58	0.21	0.58	1.35
G. juncifolia	0.57	0.10	0.52	1.22
A. ligulata	0.72	0.44	0.51	1.19
C. eremaea	0.66	0.16	0.50	1.18
G. cycloptera	0.59	0.16	0.50	1.17
	Phase I	**Phase L**		
T. basedowii	26.51	24.83	11.11	31.98
A. contorta	2.57	1.46	2.70	7.76
G. stenobotrya	3.86	2.70	1.79	5.16
T. glaucifolia	1.30	0.46	1.48	4.27
E. drummondii	1.25	0.20	1.40	4.04
C. balonensis	1.32	0.43	1.27	3.64
S. parvifolia	0.56	0.94	1.10	3.18
S. fibulifera	0.74	0.80	1.06	3.06
E. aristidea	0.75	0.16	0.84	2.42
E. longifolia	0.68	0.21	0.75	2.17
G. cycloptera	0.59	0.16	0.66	1.91
A. ligulata	0.68	0.44	0.60	1.72
Y. australiensis	0.44	0.12	0.53	1.54
A. dictyophleba	0.43	0.14	0.50	1.45
Sida sp.	0.35	0.16	0.48	1.38
D. radulans	0.40	0.02	0.46	1.34
S. spinescens	0.29	0.19	0.45	1.29
P. pachyphylla	0.39	0.00	0.44	1.27

aristidea, *G. stenobotrya*, and *T. glaucifolia*. The first four species were most abundant during the High population phase. *Trachymene glaucifolia* was most abundant during the Increasing phase. The 2-d MDS results for plant cover (Figure 4.14) do not show good separation between population phases despite low stress, although ANOSIM results between phases were significant (Global R=0.265, P=0.001).

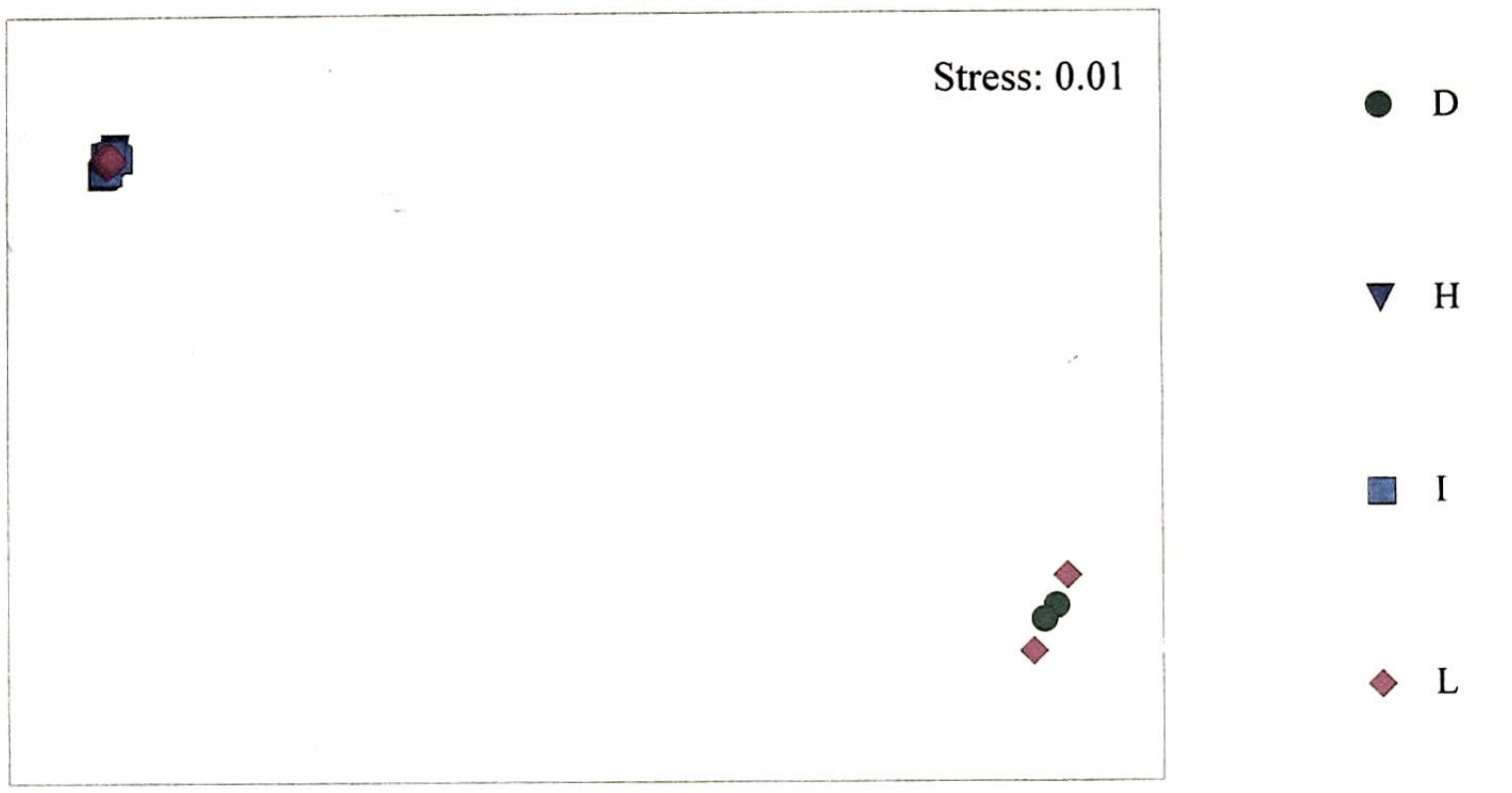


Figure 4.14. MDS comparison of plant cover between four phases of rodent population cycles. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

The pairwise tests for the four population phases showed that the Decreasing and Increasing phases were not significantly different (Table 4.18), although all other comparisons were.

Table 4.18. Pairwise ANOSIM tests between rodent population phases on the plant cover. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

Phase comparison	***R***	***P***
D vs H	0.250	0.033
D vs I	0.041	0.200
D vs L	0.215	0.007
H vs I	0.197	0.035
H vs L	0.661	0.001
I vs L	0.259	0.001

The species that contributed to differences between population phases for the seed crop index were few: *T. basedowii*, *A. contorta*, *E. aristidea*, *G. stenobotrya*, *T. glaucifolia*, and *C. balonensis* (Table 4.19). *Triodia basedowii* was most abundant during the Increasing phase. *Aristida contorta* produced seeds mainly during the High and Increasing phases. *Eriachne aristidea* seeds were observed mostly during the High phase, even if in small quantity. *Grevillea stenobotrya* also produced a small amount of seed mainly during the Decreasing and the Increasing phases. *Trachymene glaucifolia* and *Calandrinia balonensis* produced more seeds during the Increasing phase. The MDS results suggested little separation between phases for the seed crop index (Figure 4.15), and ANOSIM confirmed that the phases did not differ (Global R=0.013, P=0.363). Therefore the temporal differences between phases deduced from the rodent capture rates did not match any changes in seed crop.

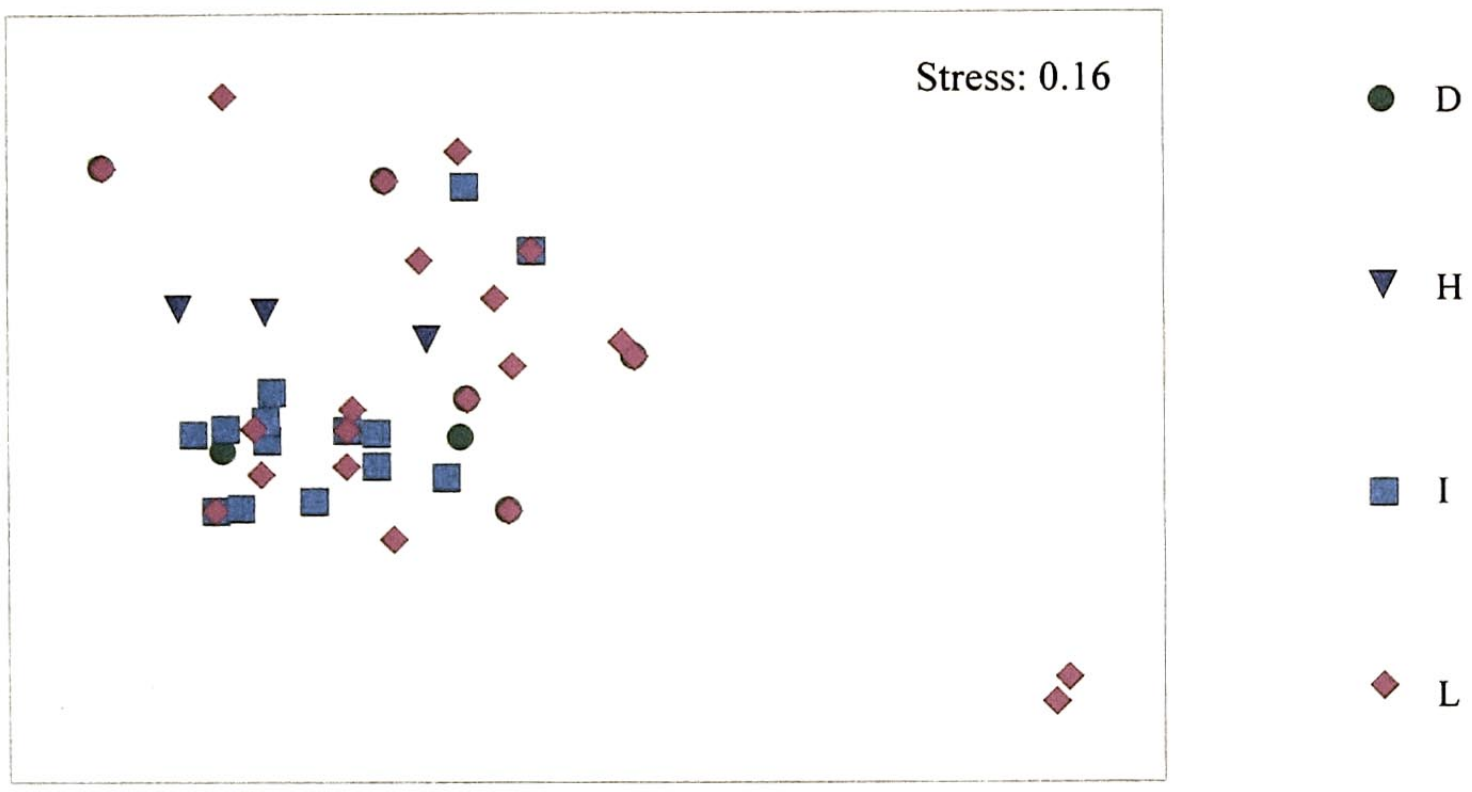


Figure 4.15. MDS comparison of seed crop index between four phases of rodent population cycles. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

The main species to affect differences in phases for the flower crop were: *E. drummondii*, *C. balonensis*, *T. basedowii*, *A. contorta* and *G. stenobotrya* (Table 4.20). *Euphorbia drummondii* produced flowers mostly during the Increasing and High phases, *C. balonensis* mostly during the High and Decreasing phases, *T. basedowii* mostly during the Decreasing and Increasing phases, *A. contorta* mostly during the Increasing and High phases and *G. stenobotrya* mostly during the High and Decreasing phases. All the species mentioned, with the exception of *G. stenobotrya*, were more abundant at the High

Table 4.19. Results of similarity terms (SIMPER) analysis on seed crop in the four population phases of the two species of study rodents. A cut-off of a cumulative % dissimilarity of 85 % was applied. Av.Abund = average abundance of species in the seed crop, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase D	**Phase H**		
A. contorta	1.98	12.81	50.54	55.58
T. basedowii	13.35	1.17	24.04	26.44
	Phase D	**Phase I**		
T. basedowii	13.35	32.13	50.83	62.94
A. contorta	1.98	4.83	9.78	12.10
C. balonensis	0.34	1.09	3.60	4.45
G. stenobotrya	0.32	0.24	3.53	4.37
	Phase H	**Phase I**		
T. basedowii	1.17	32.13	38.32	45.15
A. contorta	12.81	4.83	30.07	35.42
T. glaucifolia	0.01	1.48	2.70	3.18
	Phase D	**Phase L**		
T. basedowii	13.35	7.73	50.08	58.77
A. contorta	1.98	1.12	10.29	12.08
G. stenobotrya	0.32	0.10	8.78	10.30
T. glaucifolia	0.31	0.20	3.09	3.63
	Phase H	**Phase L**		
A. contorta	12.81	1.12	55.60	60.59
T. basedowii	1.17	7.73	18.78	20.46
E. aristidea	0.65	0.05	3.17	3.45
	Phase I	**Phase L**		
T. basedowii	32.13	7.73	51.80	60.95
A. contorta	4.83	1.12	11.03	12.98
T. glaucifolia	1.48	0.20	4.30	5.06
C. balonensis	1.09	0.08	3.86	4.54

Table 4.20. Results of similarity terms (SIMPER) analysis on the flower crop on the four population phases of the two species of study rodents. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of species in the flower crop, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase I	**Phase H**		
E. drummondii	1.72	1.19	15.24	17.63
C. balonensis	2.72	0.43	14.35	16.60
T. basedowii	10.60	0.00	12.86	14.88
A. contorta	3.28	0.97	8.42	9.74
G. stenobotrya	0.29	0.62	5.72	6.62
T. glaucifolia	1.83	0.02	5.42	6.27
S. fibulifera	0.52	0.44	3.07	3.56
G. cycloptera	0.59	0.17	2.03	2.35
E. aristidea	0.85	0.09	1.90	2.20
	Phase I	**Phase D**		
T. basedowii	10.60	10.70	30.01	33.73
C. balonensis	2.72	0.91	16.44	18.48
E. drummondii	1.72	0.71	9.74	10.94
A. contorta	3.28	0.93	6.05	6.80
T. glaucifolia	1.83	0.54	5.56	6.25
S. fibulifera	0.52	0.13	2.90	3.26
	Phase H	**Phase D**		
T. basedowii	0.00	10.70	26.66	28.38
E. drummondii	1.19	0.71	24.16	25.72
G. stenobotrya	0.62	0.46	9.20	9.80
A. contorta	0.97	0.93	5.92	6.30
C. balonensis	0.43	0.91	4.44	4.73
S. fibulifera	0.44	0.13	2.70	2.88
	Phase H	**Phase L**		
C. balonensis	2.72	0.30	21.86	23.83
T. basedowii	10.60	0.01	14.23	15.52
E. drummondii	1.72	0.08	12.10	13.18
A. contorta	3.28	0.14	8.41	9.17
T. glaucifolia	1.83	0.09	6.97	7.59
S. fibulifera	0.52	0.10	4.00	4.36
G. cycloptera	0.59	0.04	2.22	2.42
Species B	0.29	0.00	1.99	2.17
	Phase H	**Phase L**		
E. drummondii	1.19	0.08	33.32	35.20
G. stenobotrya	0.62	0.03	11.71	12.37
A. contorta	0.97	0.14	8.35	8.82
C. balonensis	0.43	0.30	7.07	7.47
S. fibulifera	0.44	0.10	4.22	4.46
A. ligulata	0.15	0.00	3.41	3.61
C. eremaea	0.12	0.01	3.33	3.52
M. maderaspatana	0.09	0.00	2.89	3.05

continue

Table 4.20. continued

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase D	**Phase L**		
T. basedowii	10.70	0.01	32.38	34.98
C. balonensis	0.91	0.30	15.26	16.48
S. fibulifera	0.13	0.10	8.93	9.65
A. contorta	0.93	0.14	6.80	7.35
E. drummondii	0.71	0.08	6.74	7.28
Sida sp.	0.02	0.01	3.20	3.46

compared to the Low phase. The MDS results showed little evident separation (Figure 4.16), and were associated with only moderate stress, but the ANOSIM was significant (Global R=0.209, P=0.001).

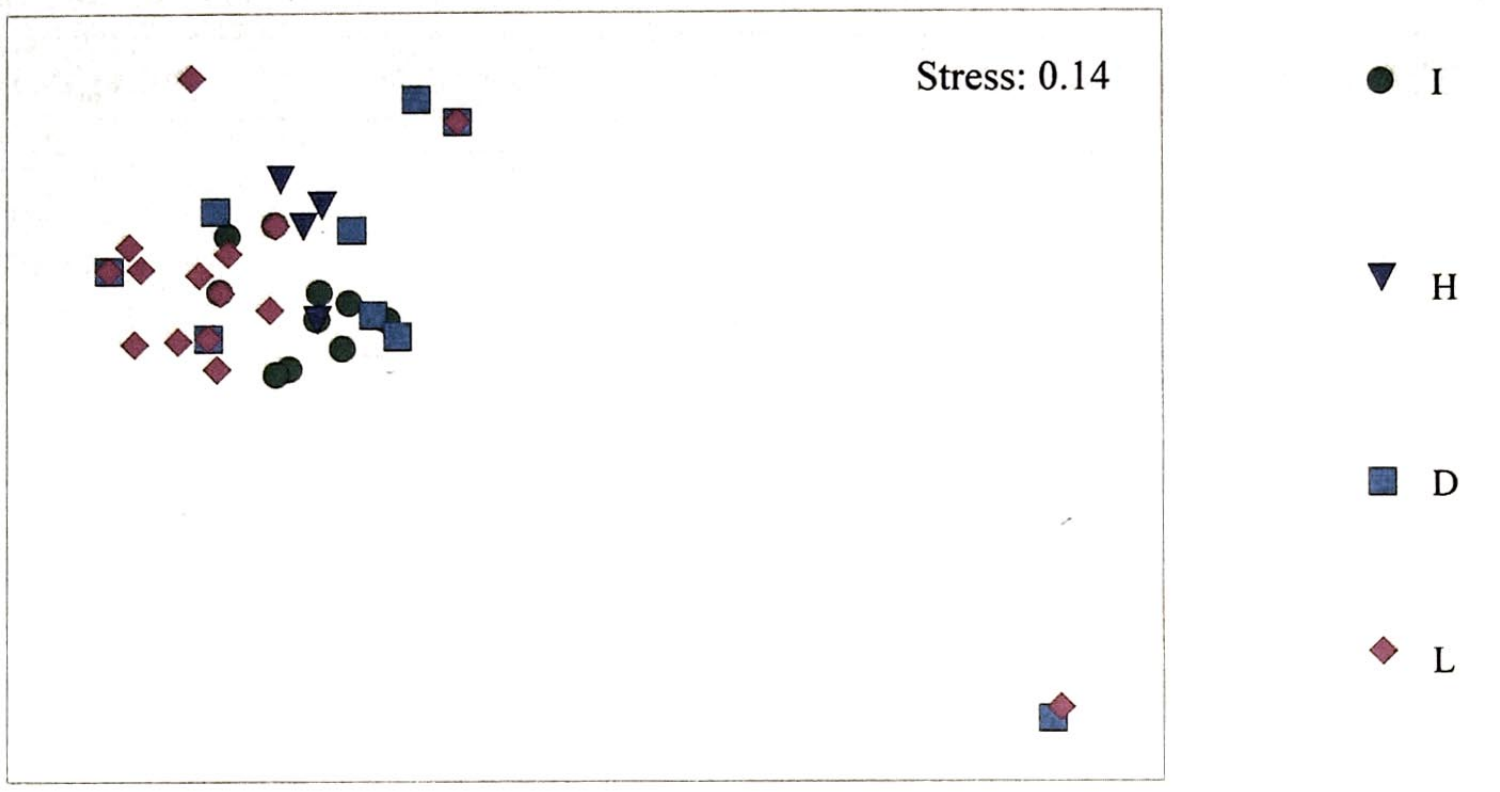


Figure 4.16. MDS comparison of flower crop index between four phases of rodent population cycles. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

Pairwise tests indicated that the Decreasing and High phases and High and Increasing phases were not significantly different with respect to flower crop (Table 4.21), but other phases differed strongly.

Table 4.21. Pairwise ANOSIM tests between rodent population on flower crop index. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

Phase comparison	***R***	***P***
D vs H	0.076	0.212
D vs I	0.231	0.006
D vs L	0.227	0.001
H vs I	0.101	0.125
H vs L	0.269	0.018
I vs L	0.190	0.020

Table 4.22 shows the SIMPER analysis for seed abundance in soil samples. The main species that differed between phases were *T. basedowii*, *T. glaucifolia*, *E. aristidea*, and *H. floribundum*. The abundance of *T. basedowii* seeds in the seed bank was highest during the

Table 4.22. Results of similarity terms (SIMPER) analysis on seeds in soil samples in the four population phases of the two species of study rodents. A cut-off of a cumulative % dissimilarity of 80 % was applied. Av.Abund = average abundance of seed species in the soil samples, Av.Diss = average dissimilarity, Contrib% = percentage contribution to multivariate difference between groups. Phase D = Decreasing phase, Phase H = High phase, Phase I = Increasing phase, Phase L = Low phase. Full names of plant species are given in Appendix 3 (Table 1).

Food categories	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Contrib%**
	Phase D	**Phase H**		
T. basedowii	6.66	30.68	32.59	49.86
E. aristidea	1.39	8.12	9.06	13.87
E. drummondii	3.81	0.78	4.15	6.36
T. glaucifolia	4.75	1.41	3.97	6.07
	Phase D	**Phase I**		
T. basedowii	6.66	18.31	12.25	18.32
T. glaucifolia	4.75	19.93	11.61	17.36
H. floribundum	0.73	15.68	8.09	12.10
G. cycloptera	1.11	6.34	5.65	8.44
E. drummondii	3.81	0.43	3.70	5.54
Maireana sp.	0.06	8.05	3.33	4.98
S. fibulifera	2.65	4.96	2.92	4.37
A. contorta	1.61	2.00	2.38	3.56
C. erinacaea	0.00	1.95	2.31	3.46
	Phase H	**Phase I**		
T. basedowii	30.68	18.31	19.50	29.14
T. glaucifolia	1.41	19.93	11.60	17.33
H. floribundum	0.00	15.68	7.33	10.95
E. aristidea	8.12	2.20	5.22	7.79
G. cycloptera	0.49	6.34	4.41	6.58
A. contorta	4.22	2.00	3.03	4.53
	Phase D	**Phase L**		
T. basedowii	6.66	21.22	15.14	24.27
T. glaucifolia	4.75	15.51	8.89	14.25
H. floribundum	0.73	11.96	7.83	12.55
S. fibulifera	2.65	5.88	3.73	5.97
E. drummondii	3.81	1.67	3.70	5.93
A. contorta	1.61	4.09	3.38	5.42
S. parvifolia	0.35	2.63	2.28	3.66
G. cycloptera	1.11	2.84	1.91	3.06
C. erinacaea	0.00	1.68	1.77	2.83
	Phase H	**Phase L**		
T. basedowii	30.68	21.22	22.38	34.90
T. glaucifolia	1.41	15.51	9.32	14.54
H. floribundum	0.00	11.96	6.85	10.68
E. aristidea	8.12	1.51	6.22	9.70
S. fibulifera	1.88	5.88	2.87	4.47
S. parvifolia	0.16	2.63	1.86	2.90
A. contorta	4.22	4.09	1.65	2.58

continue

Table 4.22. continued

Food categories	Av.Abund	Av.Abund	Av.Diss	Contrib%
	Phase I	Phase L		
T. basedowii	18.31	21.22	13.56	22.66
T. glaucifolia	19.93	15.51	9.51	15.89
H. floribundum	15.68	11.96	8.49	14.18
G. cycloptera	6.34	2.84	3.78	6.31
Maireana sp.	8.05	3.24	3.56	5.94
S. fibulifera	4.96	5.88	2.78	4.64
A. contorta	2.00	4.09	2.47	4.14
N. spodiotricha	3.91	2.04	1.74	2.90
S. parvifolia	0.20	2.63	1.64	2.74

High, Low and Increasing phases. *Eriachne aristidea* seeds were also most abundant during the High phase, followed by the Increasing phase. *Trachymene glaucifolia* and *H. floribundum* seeds were mostly present during the Increasing and Low phases. Figure 4.17 shows the results of the MDS for this food resource, and indicates no evident patterning.

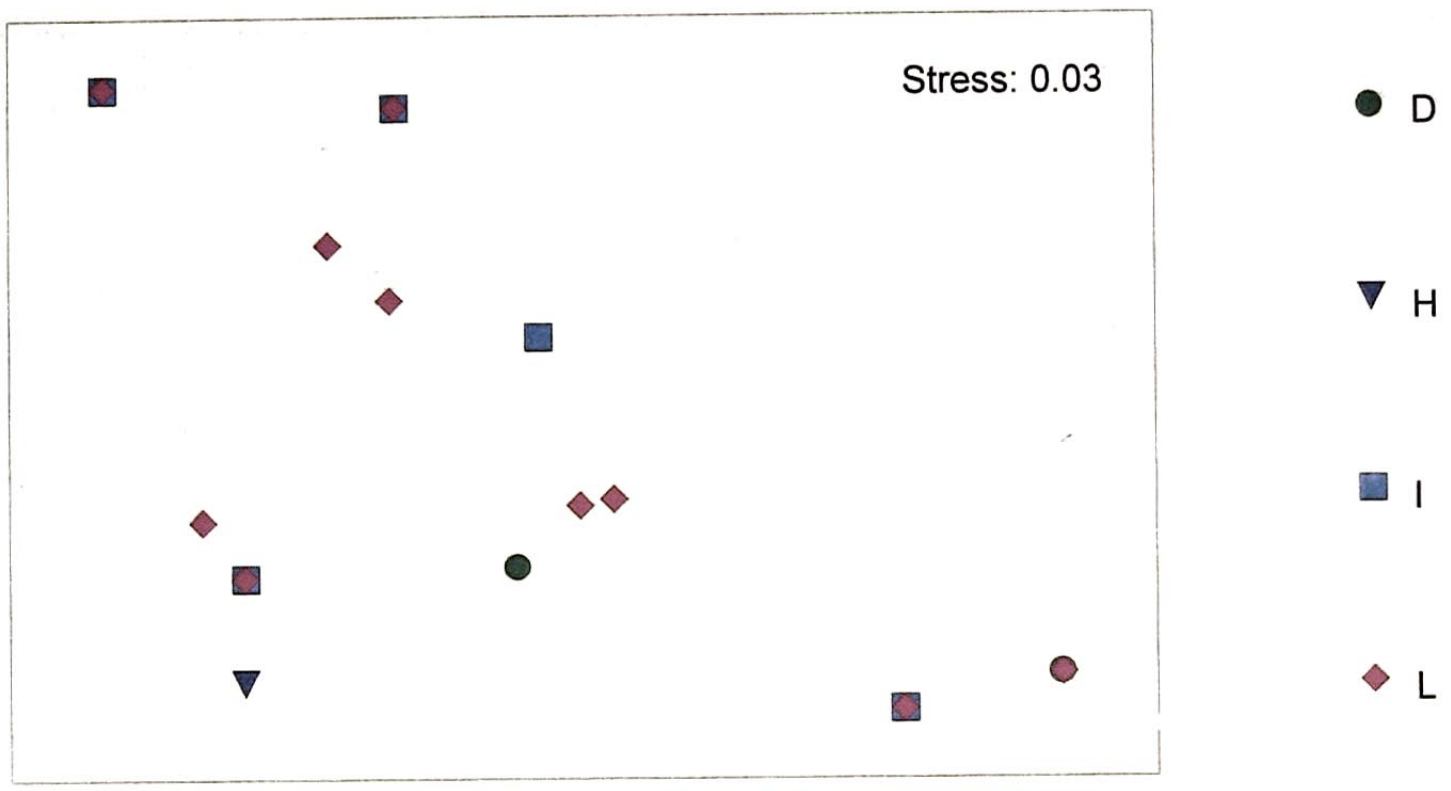


Figure 4.17. MDS comparison of seed samples from soil samples between four phases of rodent population cycles. D, Decreasing phase, H, High phase, I, Increasing phase, and L, Low phase.

The ANOSIM for the soil seed abundance was not significant (Global R=0.076, P=0.221), indicating little difference in soil seed composition between rodent population phases.

When population phases were compared between the two species, they were highly similar with respect to each food resource (plant cover Global R=-0.026, flower crop Global R=-0.032, seed crop Global R=-0.028, soil samples Global R=-0.077, P>0.05 for all).

Finally, correlations between food resources were not significant (r-values ranged from −1 to 0.988, P>0.05 for all). It is likely that a non-linear relationship exists between food resources or that despite the extremely high r-values, the correlations were non-significant because of low sample size.

4.3.5. Do dietary changes reflect food resource changes during different population phases?

When the results of these latter SIMPER analyses on food resources are compared with the SIMPER analysis on the gut contents, similarities for same phases are not very strong. Only a few species contributed to observed similarities, such as *T. basedowii* and *T. glaucifolia*. The pattern is similar to the one already observed in the comparison of gut contents with food resources using the PSI. It is again likely that a non-linear relationship exists between food resource abundance and what the two species of rodent eat.

4.3.6. Parasites

The gut contents of the two species contained endoparasites, probably Nematoda. Parasite abundance varied depending on population phase and rodent species (Figure 4.18).

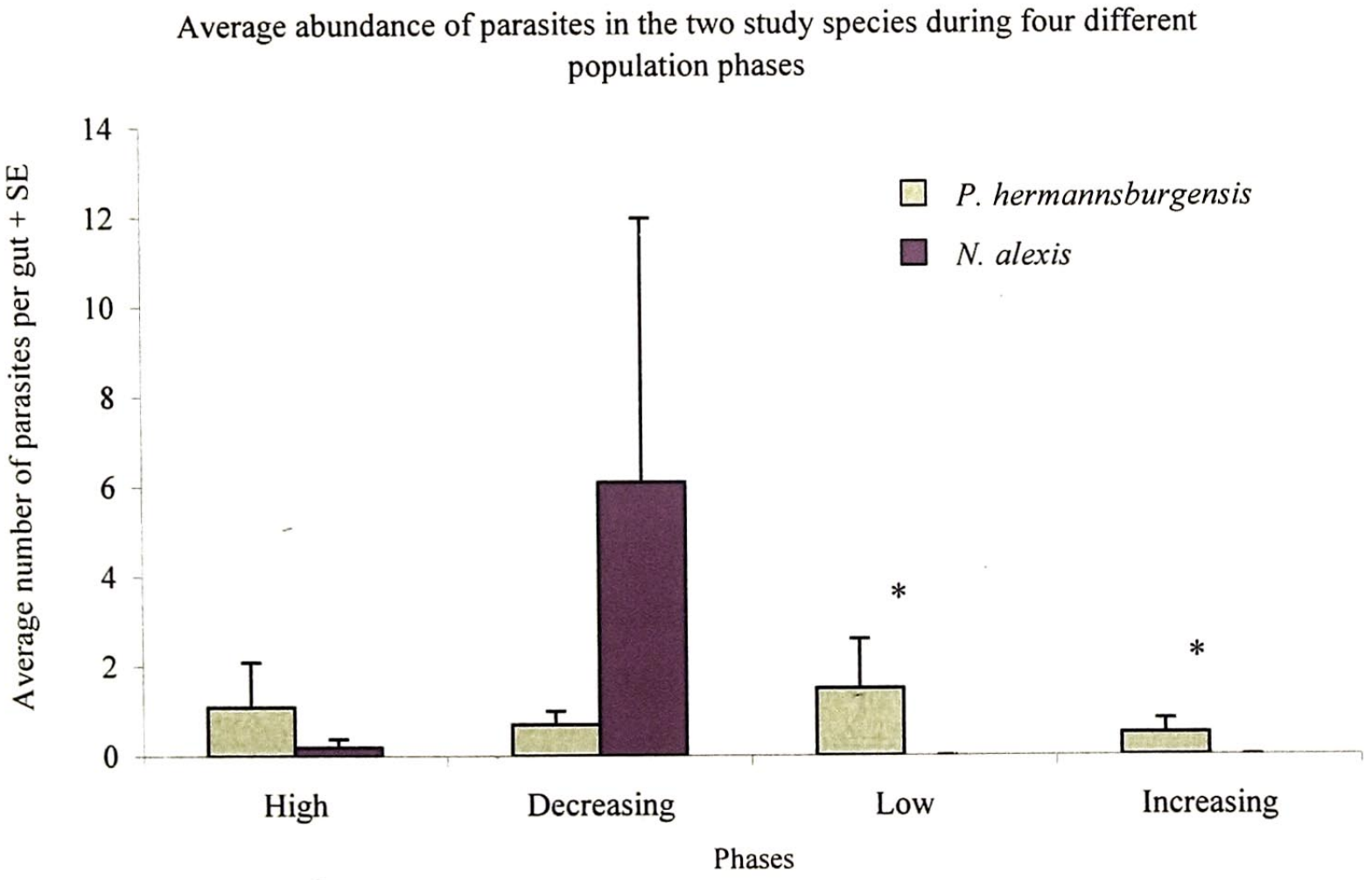


Figure 4.18. Comparison of the average abundances of parasites in guts of the two rodent species during different population phases. The Mann-Whitney test was used to test any differences in representation. * $P< 0.05$.

In the Low and Increasing population phases *P. hermannsburgensis* had more parasites on average in their guts than *N. alexis* (U=25.00, P=0.013, and U=36.00, P=0.018,

respectively). *Pseudomys hermannsburgensis* guts contained parasites consistently over the four phases, whilst those of *N. alexis* had parasites only during the High and Decreasing phases. The high number of parasites during the Decreasing phase was mostly due to two *Notomys* individuals whose guts each contained over 30 parasites. Such high numbers of parasites may be related to decreases in individual condition (Feore *et al.* 1997, Begon 2003), although sample sizes were too low to know whether parasitism had any impact on population numbers.

4.4. DISCUSSION

4.4.1. Main findings of Chapter 4

The results of this chapter show that diets changed dramatically during population fluctuations of the two study species of rodents. Food resources appeared to change, too, even if not with the same patterns found in the diet.

Differences between the diets of the two species were observed. Seeds, Plant material and Invertebrates represented the main food categories in the diets although seeds were exploited similarly by the two species during equivalent population phases. The phases that showed the most differences were the High and Low phases during which the two rodent species appeared to use different foraging strategies. The two species differed slightly in the quantity and the quality of foods that they ate, and such differences were variable during their population cycles. These findings agree generally with the study on the two species by Murray and Dickman (1994a).

Plant cover was correlated with rain with a 4-6 month time lag, and food resources also followed rainfall with a 0-2 month time lag. Moreover, rain was also correlated with plant cover species diversity with a one-month time lag. Rodents appeared to respond to changes in abundance and quality of cover. No response was observed by *N. alexis* to changes in food resources, but *P. hermannsburgensis* appeared to respond to fluctuations in the seed crop with a 3-month time lag, and to changes in the flower crop with a 9-month lag. It did not respond to fluctuations in plant species diversity. There was little evidence that diet changed in a linear way with cover. However, dietary differences were evident during the different phases of the rodents' population cycles. Rodent diets were strongly correlated with some food resources, even if the patterns differed between the two species. However, there was little overlap between diets and food resources at different phases of the

population cycles. No correlations were observed between food resources. The abundance of parasites changed between different population phases, appearing relatively constantly in *P. hermannsburgensis* guts, but being present only during the High and Decreasing population phases in *N. alexis*.

4.4.2. Rodent diets

As found by Murray and Dickman (1994a), the diets of the study species differed significantly during the phases of their population cycles. Dietary shifts from some food categories to others may be due to differential availability and accessibility during different population phases. However, it is important to remember that dietary analyses are always subjected to biases (e.g. Smith & Shanduk 1979, Holechek *et al*. 1982, Lechowicz 1982, McInnis *et al*. 1983, Putman 1984, Dickman and Huang 1988, Norbury 1988a, b, Loggers 1991, Norbury and Sanson 1992, Hughes 1993, Campos 1997). For example, seeds were identified by their husk characteristics, however some husks were probably more cryptic, digestible, or less noticeable than others. Besides, mice could differentially discard some husks before ingestion. In addition, a high proportion of the diet was plant material that was impossible to identify. Consequently, many seed species may have been eaten undetected, and hence have been underestimated. For this reason, any interpretation from these data must be very cautious. Nevertheless, gross patterns of usage of some food categories could be deduced and even finer patterns for some species could be identified.

In the High phase, when rodent densities were at their maximum, *P. hermannsburgensis* became more selective and decreased its diet niche breadth, while *N. alexis* became more generalist and expanded its niche breadth, contradicting the prediction that animals should be more selective when food resources are abundant (Pulliam 1974). Consequently, dietary overlap between the two species was least during the High phase. In this case, *N. alexis* may have had a suppressive effect on *P. hermannsburgensis*, which could have avoided competition by reducing its niche breadth and taking foods avoided by the larger species. Competition can influence the diet of an animal by changing its foraging behaviour (Pimm *et al*. 1985). It is likely that during the High phase, food resources started to decrease both because they were overexploited by the population at high density and because of the lack of new input of water to trigger further primary production. Thus, small overlaps during the High and Low phases may be an indication of food resource scarcity and partitioning for coexistence. Luo and Fox (1996) stated that coexistence between two

species might occur when resources and habitat favour neither species, while competitive displacement or dominance of one species by another might be observed when food resources or habitat conditions favour either species. However, because of the lack of experimental evidence, such as manipulation experiments, any assumption of competition between the two species must be cautious. In addition, *N. alexis* and *P. hermannsburgensis* tend to use different microhabitats, open areas for the former species and spinifex hummocks for the latter (Murray and Dickman 1994a); thus it is possible that dietary segregation between species occurs primarily via microhabitat usage. In fact, Schoener (1974) stated that partitioning habitat, rather than food resources, represented a primary mechanism for the coexistence of small mammals, and this has been affirmed by several subsequent authors (e.g. Goldingay and Price 1997, Morris 1999, Maitz and Dickman 2001). Differential microhabitat use may also explain differences in the two species' diets (Murray and Dickman 1994a). During the High phase when both rodent species' densities were high, it is likely that resource partitioning via microhabitat segregation becomes more and more difficult due to intraspecific interactions, and interspecific interactions then become more frequent. Consequently, changes in foraging behaviour may take place to minimise possible competition (Ylönen *et al.* 2002). Moreover, an eventual increase in plant cover may reduce the preferred microhabitat for *N. alexis* and enlarge it for *P. hermannsburgensis*, thereby disadvantaging the former species and leading to changes in its foraging behaviour.

During the Decreasing and Increasing phases, the two species seemed to adopt similar dietary strategies that caused strong dietary overlap. The two species might have been using different microhabitats at those stages, because the available food resources were probably widespread and enough to sustain populations of both species. In fact, during the Decreasing phases, small numbers of rodents were exploiting the available food resources so that per capita demands may not have been severe at these times. It is also possible that during the Increasing phases free water was accessible and available in larger quantities, and the pressure to maximise water intake, with its related consequences (e.g. higher dietary selectivity, feeding on metabolic water-rich food items, avoiding lipid-rich food items), was released. Consequently, Decreasing and Increasing phases seemed to be the crucial periods during which the peaks or troughs of the populations were determined, because extrinsic (food limitation) and intrinsic (high density) suppressive factors were relaxed.

It appears that the main differences between population phases are driven by the availability of Invertebrates, Fruits and some seed species (e.g. *T. glaucifolia*, Chenopodiaceae, *G. cycloptera*) in the case of *N. alexis*, and by Invertebrates and some seed species (e.g. *T. glaucifolia*, *T. basedowii*, *P. polystachyus*, *D. radulans*) in the case of *P. hermannsburgensis*. The two species showed differential use of Invertebrates and Fruits during the Low and the High phases. It is likely that Fruits and Invertebrates represent important food categories, rich in free water, vitamins, and proteins, and have considerable nutritional value, thus the two rodent species exploited them similarly. In fact, Murray and Dickman (1994b) found that both rodent species preferred Invertebrates to seeds and plant material in a captive situation. For reasons of practicality, this thesis is focused on the granivorous portion of the diet of the two species, and very little information was obtained on Invertebrates. Nevertheless, it will be worth further exploring this food category as it appears to represent an important dietary staple for these rodents, especially during certain periods of their cycle. Parasites are also worthy of closer study. They are virtually absent during certain population phases, but abundant during others (see Figure 4.18; *N. alexis*, Decreasing phase), and potentially may contribute to the decrease in population numbers.

Some gross differences in diet (plant family, type and survival stage) existed between the two rodent species. These patterns may be explained by differential microhabitat use of the two species, and by differential availability of foods between population phases. For example, after rainfall events annuals germinate rapidly, mostly as new grasses and forbs. These plant materials represent a high quality food resource, richer in nitrogen and water than seeds from perennial shrubs (White 1993, 2002). During the High phase, *N. alexis* consumed more Annual seeds than *P. hermannsburgensis*, which in turn consumed more Invertebrates. This may be another example of food partitioning, because both these food categories represent high quality resources.

Considering the number of food items present in the diets of the two rodent species (an average of 32 for *N. alexis* and 24 for *P. hermannsburgensis*) and the number of species found in plant surveys (196) and in the soil samples (53), the rodents appeared to be selective in their diet. These results agree with the findings of Murray and Dickman (1994a) who found that the two rodent species ate only nine different species from the available total of 30. It is interesting to note that although spinifex is the dominant species at the site, and would be expected to figure largely in the diet, it doesn't. In addition, the two rodent species seemed to discard other seed species present in great abundance in the study site (e.g. *A. contorta*), thus not appearing to be opportunistic in their dietary

behaviour. They seemed to be selective (see Tables 4.15-4.16) even during periods when food resources were scarce (High and Low phases). Their strategy could be to maximise the quality of their diet with cautious selection among the foods available, rather than to maximise the food intake of the most available species. It would therefore be of interest to analyse rodent foraging behaviour more closely in regards to seed selection in order to understand better the patterns of diet choice that they exhibit. This will be dealt with further in later chapters of this thesis.

No differences in diet were found between sexes, and only small differences were observed between individuals of different reproductive condition. Pregnant females appeared to consume foods in some categories more than other adult individuals, and it is likely that these foods were richer in some nutrients necessary to sustain pregnancy. For example, pregnant *N. alexis* females consumed more 'animal remains' than other adults. Pregnant females may scavenge for animal proteins during pregnancy, and benefit from eating the remains of small reptiles and mammals found in the environment. However, due to the small sample size of this analysis, these findings must be interpreted cautiously.

4.4.3. Models 2 and 3 and their interpretations

4.4.3.1. The importance of cover (Model 2)

The results of this chapter are complex and hence not amenable to simple interpretation. Models 1, 2 and 3 presented three possible scenarios to explain the results of Chapter 3. Model 1 was already discarded on the basis of evidence presented in the Introduction of this chapter. Models 2 and 3 were tested in this chapter by different analyses and comparisons. Model 2 proposed that rainfall increases cover which in turn increases population numbers of rodents. In this model, cover is seen as a source of refuge, and not as a food resource. An increase in cover can facilitate rodents in escaping predators (Brown *et al.* 1994b, Kotler *et al.* 1994), in exploiting a greater range of microhabitats, and in improving burrowing conditions due to the softening of soil by growth of plant roots and the increased integrity of sand needed for burrowing. Several studies have shown that cover or litter manipulation can change mammalian abundance and distribution (Kitchener 1972, McMurry *et al.* 1994, Price *et al.* 1994a, b, Cox *et al.* 2000, Masters *et al.* 2003). The correlations presented in this chapter showed that cover is correlated with rainfall and so too are the capture rates of *N. alexis* and *P. hermannsburgensis*. In the case of *P.*

hermannsburgensis, cover appears to have an immediate effect on capture rates. In addition, the main increment of cover during the study period was due to *T. basedowii* (spinifex), while the contribution of other plant species fluctuated without major increments. Because of the different microhabitats used by the two species (Murray and Dickman 1994a), *P. hermannsburgensis* might get an instant advantage from an increase in cover, by being able to exploit a larger area of microhabitat. As a result, this species may be more mobile and active, and consequently more trappable, but not necessarily in higher numbers. The fact that no time lag was recorded for *P. hermannsburgensis*, and that the effect of cover is immediate, may imply that no reproduction was involved in the response of this species to increases in cover. *Notomys alexis* could also better exploit its microhabitat (open areas), by using spinifex cover as corridors for movement. Consequently, the first, instant response of *N. alexis* may be similar to the one displayed by *P. hermannsburgensis*, while the other 3- and 7 month-lagged responses may involve a real increase in population via reproduction. However, not only spinifex was likely to have caused rodent responses to cover, because the two species seemed to respond equally with a 5-month delay to changes in plant cover species diversity. It is likely that a large variety of plant covers can ameliorate the desert environment in general (Bradstock and Cohn 2002).

The third prediction of Model 2 stated that diet should not change with cover, and the results partially confirmed this hypothesis. However, from the graphical comparisons of diets with plant cover, it appeared that diet did change with changes in plant cover, but not necessarily in a linear way. The number of food categories, indicative of a changing diet, did not reflect increases or decreases in plant cover.

4.4.3.2. The importance of food resources (Model 3)

Model 3 proposed that rainfall increases food resources, which in turn increase rodent population numbers. This 'bottom-up' pattern of regulation has been reviewed by Brown and Ernest (2002). In this model, plant cover represents a food resource together with the flowers and seeds that the plants produce. Support for this model has been documented in several short- and long-term studies (e.g. Whitford 1976, Brown and Heske 1990, Brown and Harney 1993, Meserve *et al.* 1995, Madsen and Shine 1999, Ernest *et al.* 2000, Lima *et al.* 2002). What appears from the findings of this chapter is that the first step is fulfilled. Rainfall is strongly correlated with the abundance and the diversity of the main food

resources of rodents, with 0-2 month lags. Thus the desert responds to rain quickly with an increase in abundance and variety of primary producers. Similar correlations have been shown in other studies (Hillel and Tadmor 1962, Rosenzweig 1968, Fuentes and Campusano 1985, Jaksic 2001). In regards to the second prediction of the model, the results were not so clear. It may be that the second step was predicated, erroneously, on a linear relationship (Brown and Ernest 2002), and that rodents respond to primary productivity in a sequence of non-linear steps that eventually cause population increases and peaks. It is likely that several reversible phases separate a population from its low-density/poor-quality stage, when the main issue for individual rodents is finding food to survive and only few individuals reproduce, to a high-density/rich quality stage, when reproduction is possible for most of the individuals and finding food is easy. The lack of significant correlations between food resources thus may help to explain why the second step of the model was not fulfilled or is not linear. Flowers and seeds are not produced straight away after rain, as is the case with vegetative growth. Nor do seed banks reflect the abundance of seeds on plants (Price and Joyner 1997). These inequalities may be due to factors such as lack of nutrients in the soil that permit effective germination (Stafford Smith and Morton 1990), seed dispersal (McIntyre 2001), and seed predation (Tischler 1998). Several recent studies have documented the failure of Model 3 and the lack of a consistent relationship between rainfall, primary productivity and rodent population dynamics (Valone *et al.* 1995, Lima *et al.* 1999, Ernest *et al.* 2000, Brown and Ernest 2002).

The results of the correlations presented here may be reinterpreted according to this new view. Thus, the rodents responded immediately to increases in cover as increases of shelter allowed them to exploit larger areas of suitable microhabitats (Model 2). Increases in cover subsequently allowed increased access to food resources that in turn provided a higher quality diet, eventually facilitating reproduction (Model 3). During the rodent peaks of 2001, spinifex was not the dominant species recorded in seed and flower crops at that stage, but cover abundance was the highest recorded, mostly due to *T. basedowii*. It is likely that spinifex was used principally as shelter rather than as a food resource.

The response of *N. alexis* to primary productivity generated by rain seemed scant or non-existent. Given that this species disappears for long periods of time (Dickman *et al.* 1999), responses may be slow even when rainfall events produce flushes of new vegetation, flowers and seeds. *Pseudomys hermannsburgensis* responded to flower and seed crop indices with a delay of nine and three months respectively. Flowers may

eventually set seeds with some delay, and seeds may trigger reproduction in rodents, thus the longer time lag with respect to flowers is easy to interpret. In fact, high abundances of seeds and flowers were recorded during the Increasing phase (October 1999 to October 2000) that preceded the rodent peaks of 2001, while the seed and flower abundances during this latter period were relatively low. Similar patterns were observed during 1991 and 1992, when seed and flower abundance was high a few months before the rodent peaks of July 1991 and 1992, and plant cover was not so abundant. In this second case the time lag between high food abundance and eruptions was much shorter (only about 3 months).

The absence of significant results in the correlations between capture rates and seeds in soil samples may be due to the nature of the soil sample data. The data set from soil samples was quite small in comparison to those from plant surveys, and some sample months did not match with months when capture rates were assessed and plant surveys carried out. In addition, most soil samples were collected using very small quadrats. Seed distribution can be spatially and temporally very patchy in desert seed banks, and small soil samples may not be representative of the real abundance and species diversity within the environment (G. Wardle *pers. comm.*, Price and Joyner 1997). It is also important to consider that rodents are mobile, sometimes travelling distances of over 14 km to obtain resources (Dickman *et al.* 1995). The plant survey data and soil samples were collected exclusively at Ethabuka. Rodents might have foraged across extensive areas (especially during low density periods) and therefore would not have been strictly linked to the food resources measured in the single, localised area. This possibility is also valid in regard to the gut contents analysis. Thus, the results from the dietary analysis may not match those for food availability from the plant survey and soil samples because of the high vagility of the study species.

4.4.3.3. Diets and food resources during different phases of the rodent population cycles

The diets of *P. hermannsburgensis* and *N. alexis* were not correlated with plant cover but were differentially correlated with the other food resources. Rodent diets and food resources were scarcely similar during different phases. In general, the rodents fed little on plant material (assessed as vegetation cover), whereas their foraging on flowers and seeds fluctuated with a maximal exploitation of seed banks.

Correlations of diet and food resources showed responses to flower and seed crops after intervals of six and seven months, respectively for *N. alexis*, and to seed abundance in

soil samples after seven months for *P. hermannsburgensis*. However, the results of these correlations are suspect due to the small number of data points. Another problem with the methodology used in the gut content analysis was that random sampling of gut contents was sometimes impossible due to the lack of availability of carcasses so that some population phases were represented by only a single month. This may mean that, in certain cases, instead of observing general results from phases of a population cycle that lasted several months, we have observed very particular patterns from a single month. It must also be remembered that the population phases were virtually separate as defined from the graphs of rodent capture rates, but such separation is very unlikely in reality as capture rates will be manifested along a continuum. This was shown from the results of the MDS and pairwise tests between phases that consistently showed that Increasing and Low phases were not significantly different. Moreover, it is likely that population dynamic phases did not closely match food resource phases. This was observed from both the graphical comparisons and from the results of the ANOSIM and pairwise tests between phases for food resources. In addition to all this, the focus of this chapter is on primary productivity (plant cover, seeds, flowers). Invertebrates represent a very important part of the diet of the two species (Murray and Dickman 1994a, b, Figure 4.7), and fruits also are an important food during certain phases. Consequently, not all food resources that rodents relied upon during their population cycles were examined in this study, and this is likely to account for some of the discrepancies observed. A large proportion of the rodents' diets was also classified under the category Plant material. This category was difficult to analyse because material in it lacked identifying characteristics. It is probable that much information was lost because of the difficulties in identifying plant material that could have represented the matching portion of plant cover in the rodents' diets. All these problems may account for why the relationship between primary productivity and rodent population numbers was not clear.

4.4.4. Other possible factors causing rodent population fluctuations

Other variables may influence the simple models presented, and may render them more complex and dynamic. Disease and parasites (Carstairs 1974, Munger *et al.* 1983, Feore *et al.* 1997, Begon 2003), predation (Newsome and Corbett 1975, Dickman 1996a, b, Mahon 1999, Lima *et al.* 2002) and social suppressive behaviours (Krebs 2003) may be crucial in regulating population dynamics, and may independently contribute to depressive

tendencies in population cycles. Feore *et al.* (1997) demonstrated that cowpox virus infection reduced the fecundity of bank voles and wood mice by increasing the time of production of their first litters, without causing any obvious disease or mortality. This may mean a 25% reduction in average fecundity for most individuals, and for those that succumb to mortality in the first months of life it may mean a reduction in fecundity to zero. Begon (2003) stated that the effect of a parasite might be contingent on extrinsic factors such as food availability or competition. He noted, moreover, that infections rose in prevalence in peak and crashing population, with a delayed density-dependence of the order of six months, and either remained at high prevalence following a crash or disappeared from infected populations. Between-species transmission was rare, even though species occupied the same habitat, and even shared burrows. The high number of parasites found in *N. alexis* guts during the Decreasing phases may imply a reduction of fecundity in the population. Consequently, parasites and diseases may play an important role in the dynamics of natural populations, perhaps becoming prominent when food is scarce and rodent density is high.

Lima *et al.* (2002) studied populations of three species of small mammals and two owls, and proposed that differential feedback structures may explain differences in the magnitude of population fluctuations of the five species. They stated that non-outbreak species are regulated mainly by intraspecific competition and limited by their food resources, and thus fit a 'bottom-up' model. By contrast, outbreaking species are regulated by climatic effects coupled with predation. When rainfall produces abundant food resources and competition for food is relaxed, the mutual feedback loop between prey and predators dominates the dynamics. Thus the magnitude of rodent responses to rainfall may be dependent on the composition of the predator guild. Ylönen *et al.* (2002) found further that at high densities mice experienced a strong trade-off between food and safety; habitat use also became more opportunistic, with mice taking greater risks in all habitats and within each habitat at the microhabitat level.

Krebs (2003) suggested that social behaviours such as territoriality, reproductive suppression, infanticide, dispersal, and recruitment might be crucial intrinsic factors in regulating rodent population dynamics. All these social interactions can affect birth, death, and dispersal rates, and thereby population density changes, especially during High and Low phases of the rodent cycle.

In any natural population of rodents such extrinsic and intrinsic factors will operate in a complex matrix and at different magnitudes according to the specific situation, some being

more influential than others during particular phases of the rodent fluctuation. For the present study species, the possible influence of these factors remains to be investigated.

4.5. Conclusions

Significant differences in the diet and usage of food resources were detected during population cycles of the two study species. Models 2 and 3 may be partly accepted, but also integrated with other intrinsic and extrinsic factors. Rainfall increases primary productivity, but the link between this and the increase in population numbers remains unclear. Rodents respond to primary productivity but with an irregular and inconsistent pattern. Several factors, both biological and methodological, may have produced this irregularity. However, cover as a source of refuge and food represents an important resource for desert rodents. Seed and flower crops appear to represent an important resource for *P. hermannsburgensis* and *N. alexis*. The two species showed different niche breadths and low dietary overlap during the High and Low phases of their populations, while overlap increased during the Decreasing and Increasing phases. Differential usage of food resources and microhabitats may assure the coexistence of the two species. *Pseudomys hermannsburgensis* and *N. alexis* were quite selective feeders even when resources were scarce. Some of the factors underlying these behaviours are examined in the next chapters.

CHAPTER 5: SELECTION OF SPINIFEX SEEDS: THE ROLE OF WATER CONTENT

5.1. Introduction

Animal populations on land are linked in a complex and non-linear way to the water supplies that come through rainfall (Brown and Ernest 2002). Consequently, rainfall is of great importance in modelling the adaptations and the behaviours of terrestrial creatures, especially when it is highly unpredictable, as in many arid regions. Chapter 4 provided an example of the complex interaction that occurs between rodents and rainfall in arid Australia.

Due to the high evapo-transpiration rates in deserts, water rarely gets stored for long periods and it therefore represents a rapidly exhaustible resource. As a result of this, desert plants and animals are adapted to exploit water resources as efficiently and as soon as possible, with many exhibiting classical patterns of boom-bust dynamics. Numerous physiological and behavioural adaptations have evolved in animals that enable them to live in desert ecosystems (see General Introduction). One of the behavioural characteristics is the ability to actively detect and select for water, especially when foraging for food. An important characteristic that food has to possess for desert animals is the presence of water, either as metabolic water or as free moisture. Animals need to maximise their water intake whenever possible in arid environments (Frank 1988b).

During dry periods, small amounts of water can be stored in plant parts such as leaves, stems, other green material and seeds. The latter usually constitute an important proportion of the diet of desert rodents (Murray and Dickman 1994a, Murray *et al.* 1999). Morton and MacMillen (1982) stated that, besides always possessing a threshold minimum water content, even when exposed to arid conditions, seeds are highly hygroscopic and thus have the ability to absorb water from the surrounding environment. Some studies (Schmidt-Nielsen and Schmidt-Nielsen 1952, Reynolds 1958, Schmidt-Nielsen 1964, Reichman *et al.* 1986, Frank 1988a, Price *et al.* 2000) have suggested further that North American rodents may cache seeds in highly humid burrows, creating a precious reserve of damp seeds to be used during dry periods. However, the seeds may not last for long periods in such environments because they may either germinate or become mouldy (Copeland 1976). With increasing humidities, seeds can increase their water content up to 20% (Morton and MacMillen 1982). Temperature has negligible effects on moisture uptake by seeds (Copeland 1976), and larger seeds tend to contain smaller amounts of preformed

water (Morton and MacMillen 1982). Frank (1988b) found that for banner-tail kangaroo rats, *Dipodomys spectabilis*, the minimal seed water content needed for animals to maintain a positive water balance is 10%-11% wet mass, under laboratory conditions.

Another important source of water is the metabolic water that can be oxidised from seeds. When carbohydrates are oxidised, they produce a net water gain. Metabolism of lipids produces a net metabolic water gain when seeds are moist, but a net water loss when seeds are dry. Oxidation of proteins always produces severe water loss (Frank 1988b). So seeds very rich in carbohydrates are very good sources of metabolic water, while the consumption of seeds high in nitrogen and lipids, if not rich in preformed water, can severely affect the positive water balance of desert rodents. According to the study of Frank (1988b), the metabolism of grass seeds, usually rich in protein and lipid (Jones and Earle 1966), is not advantageous for a positive water balance in *Dipodomys spectabilis* until seed moisture content is at least 20% wet mass. In their natural habitat animals are likely to find seeds much drier (see Chapter 6), and so seeds which are very rich in proteins and lipids become less valuable food items if free water is not present. In order to maintain a positive water balance and to obtain other important nutrients, rodents have to compromise on their choice of food. They need to maximise their water intake through consumption of both preformed and metabolic water by always selecting the moistest seeds available. Once their water balance is positive, rodents can then exploit other food constituents, which become more valuable because of their nutrient content (Kotler *et al.* 1998).

Australian desert rodents do not cache seeds (M. Predavec *pers. comm.*, Dickman 1996c) and so lack an effective strategy to store water. In exchange they are well adapted to concentrate urine, to excrete extremely dry faeces, and to reduce their basal metabolic rate (MacMillen and Lee 1967, Lee *et al.* 1984, Dickman 1993). *Pseudomys hermannsburgensis* and *N. alexis* were found to have the most concentrated urine amongst mammals (MacMillen and Lee 1967). When experiments were performed to examine the relationship between free water availability and foraging decisions, *P. hermannsburgensis* did not appear to be affected by the presence of free water in the selection of food patches (Kotler *et al.* 1998). The foraging efficiency of these rodents was unchanged by free water, suggesting that the species may be completely dependent on the water extracted from its food. Consequently, at least some Australian desert rodents appear very skilful in detecting preformed water in their food and may select for this quality whilst foraging. By selecting for moisture they can maximise their water intake and maintain a positive water balance.

There was an inconsistent pattern shown in Chapter 4 between rainfall, food (seeds) and rodents. This could be in part because *P. hermannsburgensis* and *N. alexis* are not strictly dependent on free water from the environment, but they extract water from their food. If so they should be able to detect moist seeds. Furthermore, rodents which are not constrained by the presence of free water for their survival, are unlikely to respond directly to increases of free water from rainfall. Thus, the results of this chapter might give further evidence to discard Model 1 of Chapter 4.

The aim of this chapter is to investigate the water content selection of seeds by the two study species of rodents. I test the hypothesis that these desert rodents can detect and select the moistest seeds amongst treatments of different water content. From the results of Chapter 4, spinifex provided the most abundant cover and most copious seed output amongst desert plants. Moreover, this species was present in the diets of the two rodent species. Consequently, I chose spinifex seeds to test the ability of the two rodent species to discriminate among seeds of different water content.

5.2. Materials and Methods

Five adult female and five adult male *P. hermannsburgensis* and three adult female and three adult male *N. alexis* were returned from the Ethabuka study site between October 1999 and June 2000, and used in the experiments of this chapter. Animals were collected from spare grids distant from those used in Chapters 3 and 4, so that populations on the long-term study grids would not be affected. Unfortunately, one female *P. hermannsburgensis* died during the captive period, so the number of animals tested was reduced.

For the development of water content selection trials on seeds, the use of food dyes to colour code the seeds is very useful for marking different treatments (Frank 1988a, b). Before beginning the water content selection trials, I had to address some issues. The problems to overcome when working with moisture, food dyes and animals were of four main types. Firstly, I had to examine the physical properties of the seeds with respect to the colours used, and detect any variation in the interaction between seed water content and different colours. Secondly, I had to define a range of different levels of water content to offer to the animals. Thirdly, I had to be sure that the levels chosen maintained significantly different moisture levels within the seed over the period of the trial. Finally, I had to consider whether the mice showed preference or avoidance of some colours in pilot studies.

Spinifex (*T. basedowii*) seeds were used in the selection trials. Because it was impossible to rely on the unpredictable natural production of seeds in the desert, husked spinifex seeds were obtained from Kimseed Environmental Pty. Ltd., Western Australia.

5.2.1. Calibration curves

In order to address the first issue, I used four colour dyes to have a range of choice and I prepared different types of calibration curves, one for each possible colour (green, yellow, red, blue) that I was going to use in the experiments, and one calibration curve for the control (uncoloured seeds) using the air-oven procedure (Hart *et al*. 1959). Equal amounts of spinifex seeds (2.50 g), assessed as being the maximum consumption by an animal in one night (MacNaught 1994), were dyed in glass Petri dishes with three drops of food colour for green, yellow and blue, five drops for red, and three drops of water for the control (~ 0.12 g). The number of drops differed between colours because of their specific weight. This was imbibed in 3ml of tap water for one, two or three days, and then put in an oven at 70° C. This temperature was chosen to minimise any possible effect of high temperatures on the chemical composition of the seeds (Hart *et al*. 1959). Four replicates of each colour and the control were prepared. After ½ hour the seeds were extracted from the oven, placed for 10 minutes in a desiccator, weighed on a four digit electronic balance for the first measurement, and then put back again in the oven. Subsequent periodic measurements were recorded for each colour and the control until the treatments were completely dry. The mass of the treatments at different times was plotted to create reference calibration curves. After analysing the results, one day of imbibition was chosen as most appropriate for the study, because seeds imbibed for two and three days developed mould; similar findings have been obtained in previous studies (Hart *et al*. 1959, Reichman and Rebar 1985, Frank 1988a). Moreover, patterns of water loss for different colours were different at two and three days of imbibition. The proportion of water in each seed-colour treatment (W_f) at different times was expressed in grams, and calculated with the following formula:

$$W_f = \frac{X_i - X_f}{X_i}$$

where X_i is the mass of the treatment at time i and X_f is the final dry mass of the treatment after two weeks in the oven. The water content was then expressed as an average percentage ± SD. The first part of the preparation for the final experiments involved assessing the behaviour of differently coloured seed treatments and their interactions with

water. Data collected were assessed for normality with the nonparametric Kolmogorov-Smirnov test, using Lilliefors's distribution, and for homogeneity of variances using Levene's test (Quinn and Keough 2002). If the tests were significant data were transformed using either the log (x) transformation, log (x+1) transformation when zeros were present, or square root transformation, by choosing the transformation that best improved the distribution of the data. If, after transforming the data, variances remained heterogeneous, alpha was set at 0.01 (Underwood 1981). Using the appropriate transformations on the results of the calibration curves for the three colours and the control, the different treatments were tested in a repeated measures analysis of variance at different times to compare their pattern of water loss in the oven over a 24 hour period.

To address the second issue, above, treatments extracted after ½ hour, 1 hour and 2 ½ hours from the oven were chosen initially for their different water contents. In order to be sure that seeds with these three water levels were significantly different from each other, ten replicates from each water level (1/2 hour, 1 hour and 2 ½ hours, and dry) were prepared with the following procedure. Ten replicates each of 2.50 g of randomly chosen different colours (green, yellow, red and control) were imbibed for one day, put in an oven at 70° C for ½ hour, 1 hour, 2 ½ hours respectively and then extracted, put in a desiccator for ten minutes and finally weighed. The samples were then dried completely over a two week period. Dry treatments were prepared with the same procedure and weighed at the end of the two week period. I chose to use randomly coloured samples in the four levels of water content because coloured samples were needed in subsequent trials. The colours were uniformly distributed among treatments (the same number for each treatment: three green, three control, two yellow and two red), reducing any confounding effects caused by the colour differences. Data were again tested for normality and homogeneity of variances and the appropriate transformations were applied if necessary. The data were then analysed in a one-way ANOVA with different times as factors. Tukey's test was used as the post-hoc test (Sokal and Rohlf 1995).

5.2.2. Different levels of water content

The third issue to be addressed was if the selected levels of water content remained significantly different after having been exposed to several hours of air evaporation over night (from 6 pm to 6 am), this period being likely to resemble the situation in the actual trials. To test the loss or the gain of water via evaporation or absorption in the different

glass tanks to be used for the trials, three levels of water content (1/2 hour, 1 hour and 2 ½ hours in the oven) were tested in three glass tanks (100 cm x 40 cm x 65 cm, 96 cm x 42 cm x 62 cm, and 100 cm x 38 cm x 59 cm), in the experimental room under controlled conditions (21°C, and 30 % humidity). Two replicates of each water level (six for each glass tank) were weighed and put randomly into three glass tanks (a total of 18 samples) filled with 3 cm of desert sand and weighed after ½ hour, 4 hours, 8 hours, 12 hours and 25 hours. The tanks and the sandy substrate were to be used in actual trials later with the study animals. The samples were prepared with the same procedure described above for the control, except that no food dyes were used this time to avoid possible biases. At the end of the pilot study the samples were weighed, completely oven-dried and then weighed again. The water content was calculated with the formula above. Data were again tested and transformed for normality and homogeneity of variances with the same procedures reported above. The results were analysed in a repeated measures analysis using the three levels of water content and the three different glass tanks as categorical variables. After this pilot study two levels of water content were chosen, these being produced after ½ hour (indicated hereafter as a treatment of HIGH water content) and 2 ½ hours in the oven (indicated hereafter as a treatment of MEDIUM water content). These levels were selected as being likely to be always significantly different, irrespective of any biases due to the drying procedure.

Another set of pilot trials was carried out to monitor if the HIGH and MEDIUM treatments remained significantly different from the treatments dried for two weeks in the oven (indicated hereafter as treatments of LOW water content) after several hours of air exposure. This second pilot study was conducted during two separate trials comparing HIGH treatments with LOW treatments, and MEDIUM treatments with other LOW treatments. The pilot study was carried out in the experimental room using three different colours (green, yellow, red) and the control. Three replicates of each colour and the control were used during the two trials. Treatments were prepared following the usual procedure, weighed and then exposed during the night to the air in the experimental glass tanks. In the first trial of MEDIUM and LOW treatments, masses of the samples were measured at different intervals of time (every half an hour for the first 3 hours and then every hour for the next four hours). The last measurement was recorded 14 hours after the first. In the second trial for HIGH and LOW treatments, the samples were weighed every hour for the first six hours and then after 14 hours at the end of the test. Again the samples were collected, dried completely in a 70° C oven for two weeks and water content calculated.

Results were tested for normality and homogeneity of variances, and eventually transformed with the square root transformation. Each colour treatment was tested separately in a repeated measures analysis for the two trials.

5.2.3. Pilot studies on colour selection

Frank (1988a, b) demonstrated that food colourings did not affect food selection in the rodents he tested. In order to confirm this, the final issue raised above, in my trials, I tested the two species in pilot studies with wet (HIGH) and dry (LOW) treatments to detect any changes in preference. After capture, as noted above, animals were maintained solitarily in the laboratory in large sand-filled glass tanks on a 12L: 12D photoperiod, at a relative humidity of 40% (± 20%) and temperature of 21°C ± 7°C, and fed normally on a diet of mixed dry commercial seeds, apple, lettuce, mealworms, and crickets. All the animals were kept under protocol number L04/12-98/3/2888 issued by the University of Sydney Animal Ethics Committee. Animals were able to obtain water from their food and so no free water was provided. In order to enrich the environment, branches of desert plants, wood, logs and bark were used to build shelters. To permit animals to acclimatise to their new environment after capture, a period of three weeks elapsed before they were involved in any experiment. In order to increase the probability of feeding during trials, food was removed for 24 hours before observations began. During the run of the trials, animals were first moved from their usual glass tanks to the experimental glass tanks (described in section 5.2.2) filled with 3-4 cm of desert sand. An acclimatisation period of 2-3 hours was allowed in the new tanks. Usually three animals per night were tested, one per glass tank. In a cafeteria trial four equally spaced plastic containers of 7 cm diameter and 6 cm high were stuck to the bottom of the tank with blue-tac and surrounded with sand until the edge was almost covered and the dish mimicked a sand depression. Equal amounts for each treatment seed were used (2.50 g), slightly more than any individual rodent's daily food requirement. Seeds were offered at the onset of darkness and animals were permitted to forage for 12 hours. Each seed type was first weighed and then placed in the tank in the separate containers in randomly determined positions. Remaining seeds were recovered after carefully sieving sand in the glass tank at the end of the trial; seeds left from the treatments were weighed again, put in the oven, dried completely and then finally compared. A control of three different coloured seed treatments and one uncoloured treatment was used during each trial to monitor the eventual water evaporation or absorption during the night to allow correction

of the final consumption data. The formula used to calculate the dry mass of each sample consumed (M_F) is the following:

$$M_F = \frac{[M_{wetI} - (M_{dryF} \times K)]}{K}$$

where

$$K = \frac{M_{wetIC}}{M_{dryFC}}$$

and M_{wetI} = initial wet mass of the sample (before the trial)

M_{dryF} = final dry mass of the sample (after the trial and the oven)

M_{wetIC} = initial wet mass of the control (before the trial)

M_{dryFC} = final dry mass of the control (after the trial and the oven)

Animals were never involved in trials over consecutive nights and were returned to their usual tanks after foraging. A period of rest (a minimum of three nights) was given to animals to recover. Ten *P. hermannsburgensis* (five females and five males) were first tested with three different coloured (green, yellow, red) wet treatments and one uncoloured wet treatment over three consecutive trials. Successively only eight *P. hermannsburgensis* (three females and five males) were tested again with the same experimental design for dry treatments over three consecutive nights. This was because two *P. hermannsburgensis* females were sick. After this pilot study, two colours (green and red) and the uncoloured treatment were chosen to mark different levels of water content offered to the mice. Yellow was avoided because yellow coloured seeds were very similar to the uncoloured control seeds and so were very difficult to differentiate from them.

The same procedure as with *P. hermannsburgensis* was used to test six *N. alexis* (three females and three males), but this time only two coloured treatments (green and red) and one control were used. Another variation was that this second pilot study was repeated with the same animals three times for wet treatments and three times for dry treatments, because first results did show a weak pattern of selection. Results from these pilot studies were compared using Friedman's test and Kendall's coefficient of concordance (Zar 1996). The results from the consecutive trials both on dry and wet treatments of *N. alexis* were further analysed with the same non-parametric tests to see whether there was consistency in choice by the same individuals over repeated trials.

5.2.4. Trials on water content selection

The water content selection trials were carried out using a similar procedure to that in colour selection trials. Three different levels of water content, HIGH, MEDIUM, and LOW marked with different colours, were experimentally produced following the procedure outlined above. These three levels of water content were chosen as being likely to remain separate over a period of several hours. Equal amounts of spinifex seeds (2.50 g) were imbibed for 24 hours. The seeds were then dried at 70° C for the specified periods of time. They were then extracted from the oven, put in a desiccator for 10 minutes and weighed. Samples that were extracted from the oven hours before the beginning of the trials were put in an empty desiccator to limit water evaporation or absorption from the air. All the treatments were weighed again just before the trials and then randomly placed in the containers inside glass tanks filled with sand. A control was put in the same experimental room to monitor evaporation or absorption of the treatments during the night. After the recovery of one female and the death of another, a total of nine *P. hermannsburgensis* (four females and five males) and six *N. alexis* (three females and three males) were tested overnight, for a period of 12 hours. Animals were moved to the experimental tanks 2-3 hours before the start of the trials. Each animal was tested five times, over five separate nights. The three different water levels were assigned the same marking colours within the same trial but different marking colours were allocated over the five trials to avoid possible colour bias. At the end of each trial the sand of the entire tank was sieved and the seeds left were collected, weighed and put in the oven for two weeks. The average dry mass consumed in the five trials for each treatment was calculated and represented in pie-graphs. Average consumption of seed in each of the three treatments by each animal over the five trials is presented graphically in histograms. The calculations and the analyses applied were the same as in the pilot studies. To confirm the significance of the results, the initial and final water contents of the controls were compared using one-way ANOVA for differences among the three treatments, after log- transformation of the data. One-way ANOVA was carried out on log-transformed data on the average dry mass consumed by the two sexes of the two species for each treatment, pooling together the results of the five trials. The program SYSTAT 9 (SPSS 1999) was used in all the statistical analyses.

5.3. Results

5.3.1. Calibration curves

The calibration curves of seeds imbibed for one, two and three days showed different patterns of water release upon drying (Figure 5.1).

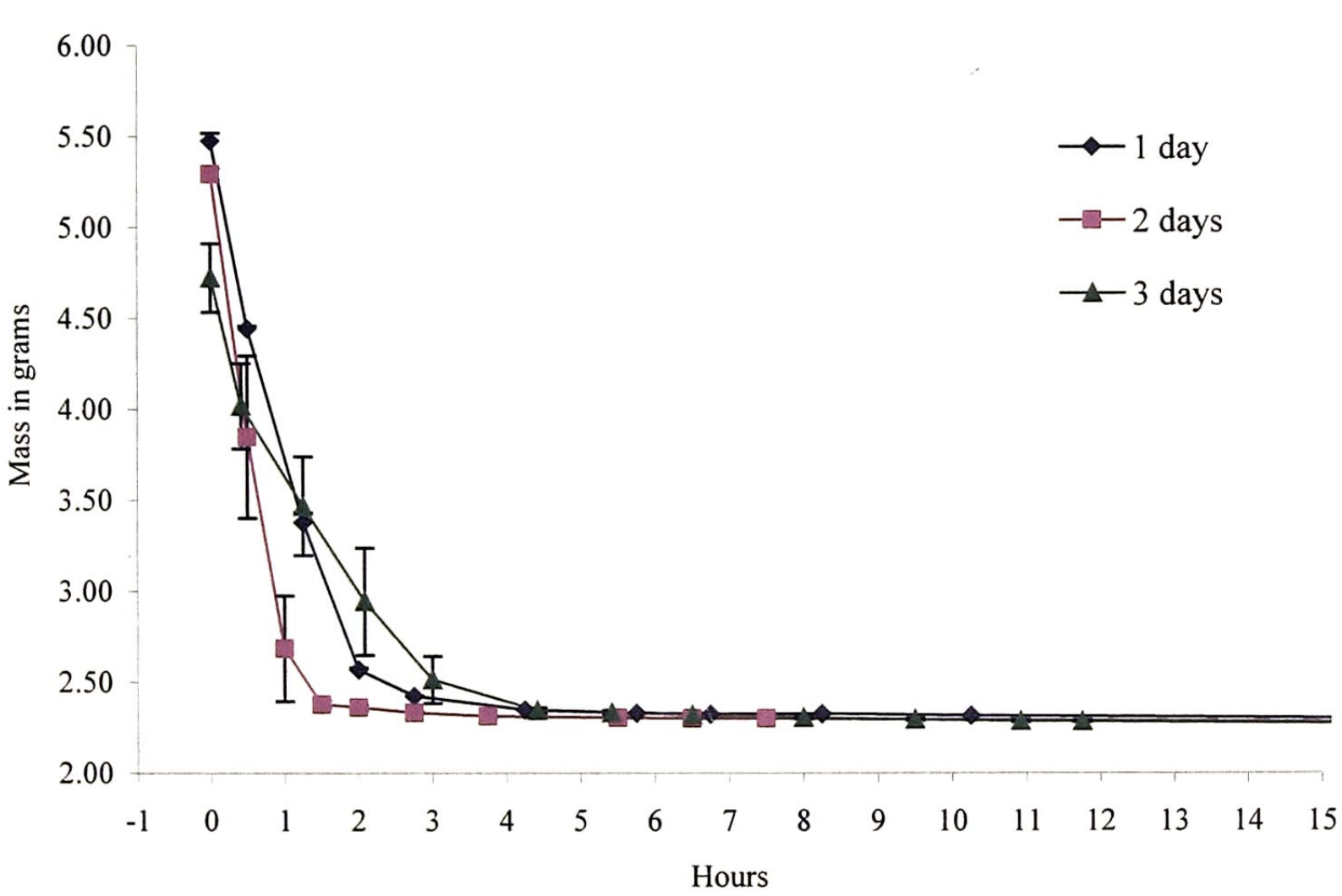


Figure 5.1. Comparison of three calibration curves obtained on uncoloured spinifex seeds put in an oven at 70°C after having been imbibed for one day, two days, and three days. The water loss is expressed as change in sample mass over time. (The pattern of water loss was similar in the green, red, yellow and blue coloured treatments, which are not depicted separately). Four replicates for each calibration curve were used, and means are shown ± SD.

Only the uncoloured seed treatment is shown because most of the coloured seed treatments exhibited a similar pattern of water release for different days of imbibition. Seeds imbibed for two and three days developed mould, as shown by previous studies (Hart *et al.* 1959, Reichman and Rebar 1985, Frank 1988a). With regards to the graphical comparisons among seed colours, all the calibration curves for different colours, except blue and green, showed very similar patterns of water loss at one day of imbibition; the

blue coloured treatment was excluded from further study due to its highly dissimilar pattern of water loss (Figure 5.2).

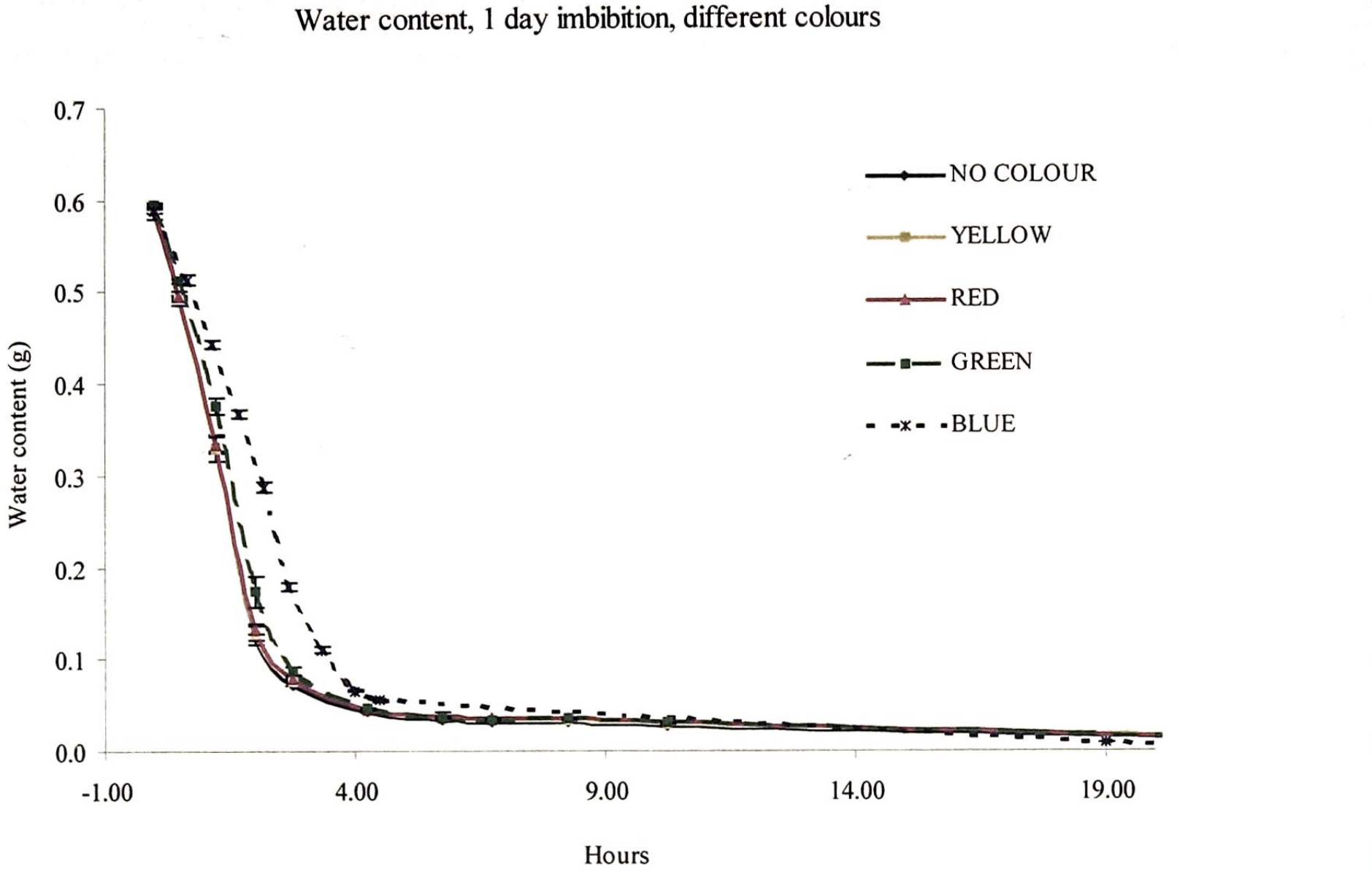


Figure 5.2. Calibration curves of four coloured treatments and one uncoloured treatment for spinifex seeds over 20 hours in an oven at 70°C. The blue coloured treatment showed a different pattern of water loss with respect to the rest of the treatments. Four replicates for each calibration curve were used, and means are shown ± SD.

A consistent pattern was not obtained at two and three days of imbibition (different curve shapes of water loss for different colours). For these reasons, for all subsequent experiments seeds imbibed for one day were used. Despite appearing to show similar patterns of water loss to other treatments, green-coloured seeds had significantly higher water content ($F_{3,8}$=20.14, P<0.001). However, the use of colours was still necessary to code different water content levels offered to the mice. Pilot studies showed that significant differences were maintained over long periods of time by the different water content treatments regardless of their colour. However, in order to minimise possible biases due to using different colours, different water content treatments were coded each time with different colours over five repeated trials. At the end of each trial the controls were analysed to be sure the water contents of the three different treatments were still significantly different.

5.3.2. Pilot studies on maintenance of different levels of water content

Four levels of seed water content were chosen because each level remained distinctly separated from the others in the calibration curves of colours. Seeds dried for ½ hour, 1 hour, 2 ½ hours and two weeks showed significantly different water content ($F_{3,36} = 94.22$, $P<0.001$). Seeds were left for two weeks in the oven to dry them completely because they appeared to keep losing water even after 15 hours, despite the initial calibration curve (Figure 5.1). In the test for evaporation under natural conditions, three levels of seed water content were analysed (1/2 hour, 1 hour and 2 ½ hours) in three slightly different glass tanks. No effect was noted for the glass tanks ($F_{2,9}$=0.311, P=0.740), but the three levels remained significantly different after 4, 8, 12 and 25 hours ($F_{2,9}$=100.15, $P<0.001$).

The results of the repeated measures ANOVA for the comparison of HIGH with LOW and MEDIUM with LOW treatments of different colours were all significant ($F_{1,3}$=23.83 to $F_{1,4}$=845.87, $P<0.05$), with the exception of the green coloured treatments. These treatments were heterogeneous even after appropriate transformation ($F_{1,4}$=18.083), and were considered not significant despite P=0.013 because the level of significance was marginally above the alpha chosen in this case (Underwood 1981). The variability of the HIGH treatments was very large, which may be due to biases in the preparation and drying procedure. Moreover, during a humid day the dry treatments were likely after six hours to absorb more water than the usual standard. In this case the difference between moist and dry treatments reduced markedly after six hours.

5.3.3. Pilot studies on colour selection

No significant selection for or against any dry colour was observed in *P. hermannsburgensis* during the pilot studies to assess the behaviour of the mice with respect to colours (χ_r^2=0.45, W=0.02, $P>0.05$). Because of the wide range of water contents produced for the wet treatments in each trial, data from animals tested on the same night were analysed separately with Friedman two-way analysis of variance and Kendall's coefficient of concordance to reduce possible noise resulting from pooling the data. On the first night only, the mice selected for the green coloured seeds (χ_r^2=8.20, W=0.91, P=0.042). No selection was observed during the other two nights for any colours (χ_r^2=1.00, W=0.11, and χ_r^2=2.70, W=0.23, $P>0.05$). No selection was observed at all by pooling together the wet data for *P. hermannsburgensis* (χ_r^2=3.36, W=0.11, $P>0.05$).

Notomys alexis also showed no selection for or against any dry colour (χ_r^2=0.08, W=0.01, P>0.05). The same analysis as in *P. hermannsburgensis* was done on six separate nights for wet treatments and on only the first night did the three mice tested show a slight selection for green-coloured treatment seeds with the lowest water content (χ_r^2=6.00, W=1.00, P=0.05). By pooling the data no selection was observed, again with the only exception of the wet, green-coloured treatments in the first trial (χ_r^2=9.33, W=0.78, P=0.009). No individual *N. alexis* showed consistent selection for any treatment over repeated trials.

5.3.4. Water content selection trials

Due to biases in the drying procedure (e.g. uneven oven temperature, different external air temparature) the three levels of water content offered to the two species were very variable. Treatments offered to *N. alexis* contained an average of 10.83% ± 4.54% SD of water for HIGH, 3.17% ± 0.29 % SD for MEDIUM, and 0.12% ± 0.17 % SD for LOW. In the case of *Pseudomys* over five trials the average water content was 15.46% ± 5.70% SD for HIGH, 4.60% ± 1.50 SD for MEDIUM, and 0.3% ± 0.78% SD for LOW.

The ability of the two species to select seeds with the highest water content offered is clearly shown in Figure 5.3. During the trials the rodents never depleted any treatment completely. *Pseudomys hermannsburgensis* appeared more likely to detect and eat seeds with the highest water content. Individuals of both species showed consistent and strong selection for seed treatments with the highest water content (Tables 5.1, and 5.2; Figure 5.4).

Table 5.1. Results of seed-water content selection trials for nine *P. hermannsburgensis* over five repeated trials. Values for Friedman two-way analysis of variance and Kendall's coefficient of concordance, degrees of freedom and *P* values are shown.

P. hermannsburgensis	**Friedman's test statistic**	**Kendall's coefficient of concordance**	**df**	***P* values**
Trial 1	18	1	2	0.000
Trial 2	17.056	0.948	2	0.000
Trial 3	13.556	0.753	2	0.001
Trial 4	13.722	0.762	2	0.001
Trial 5	14.889	0.827	2	0.001

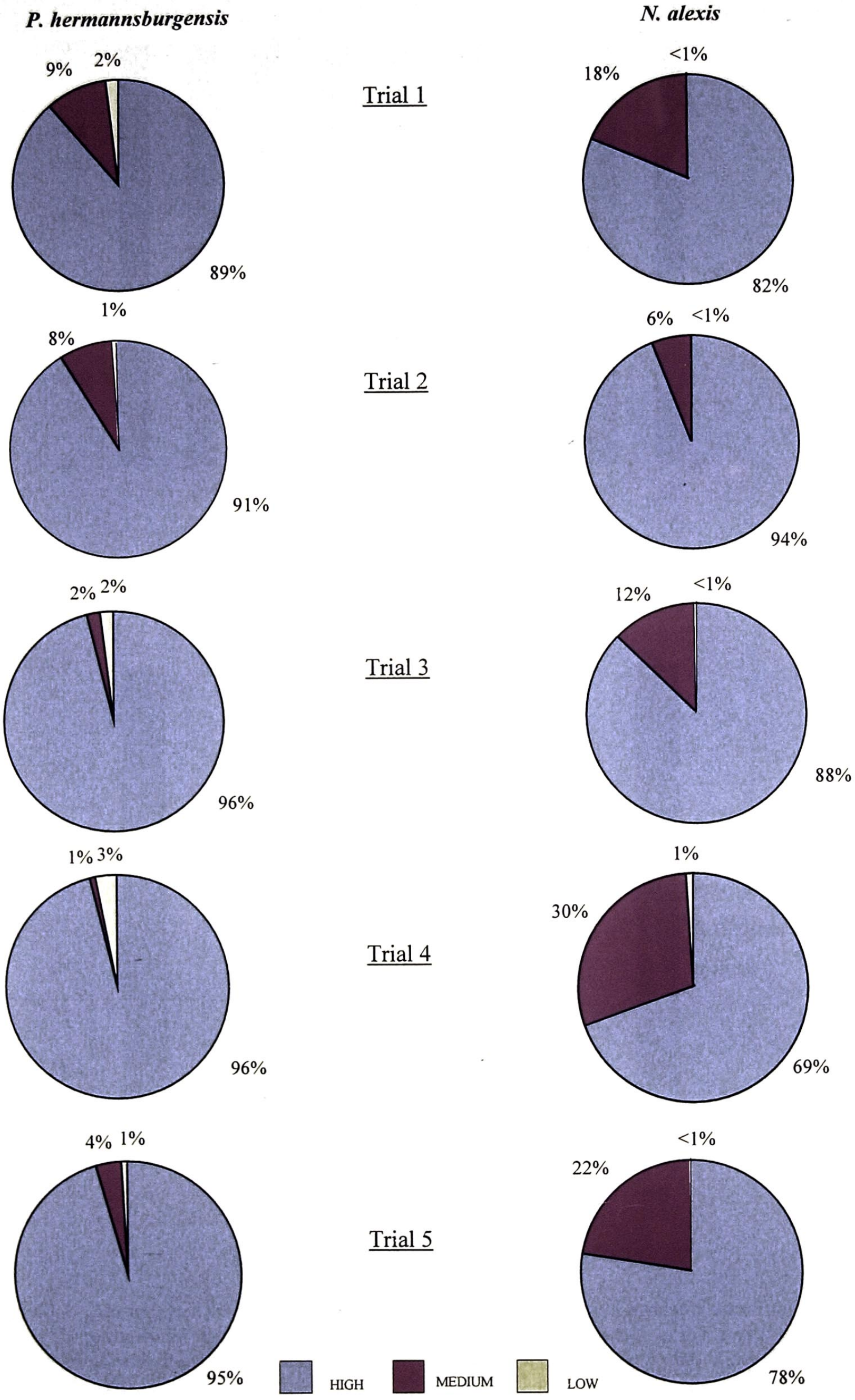
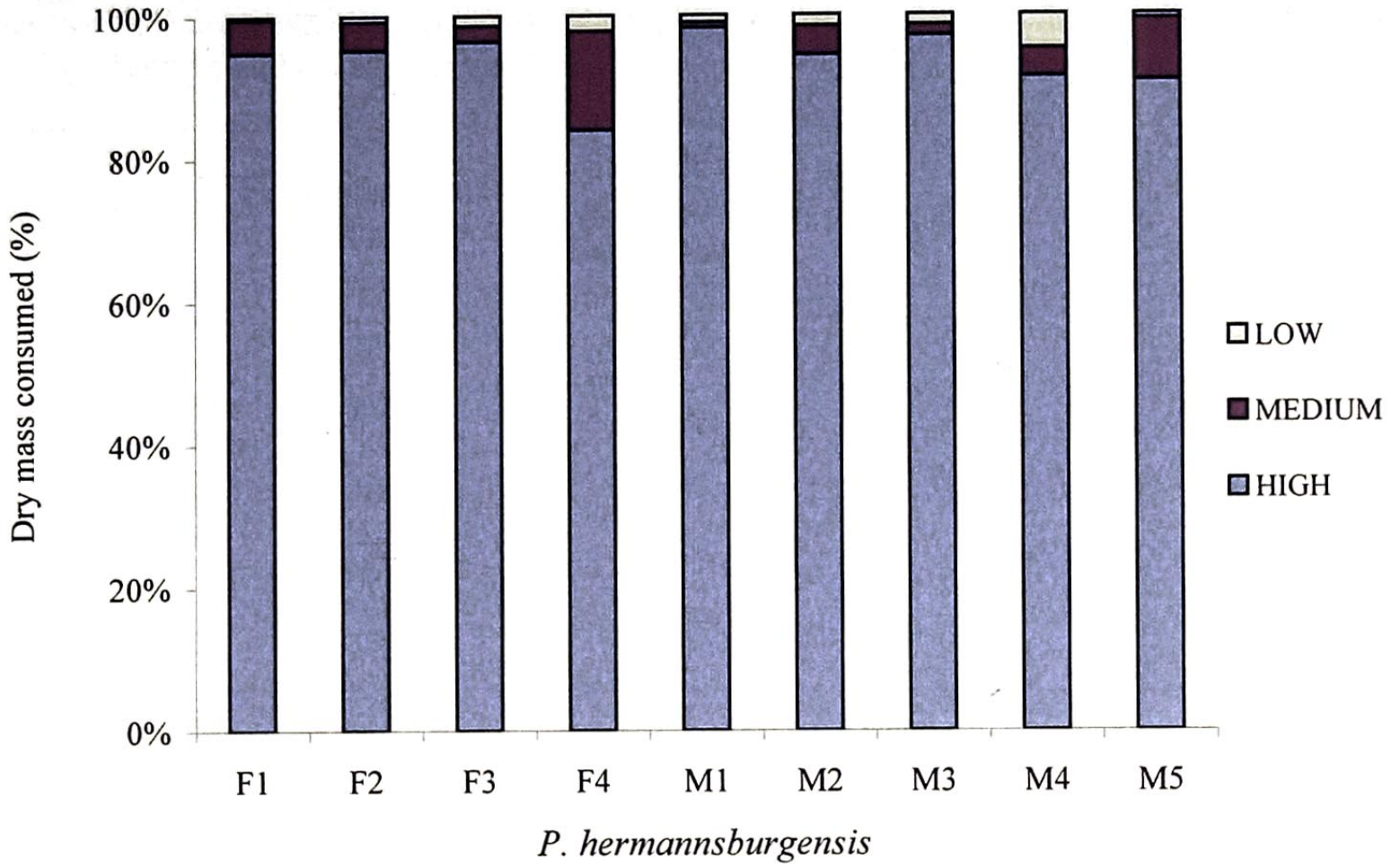
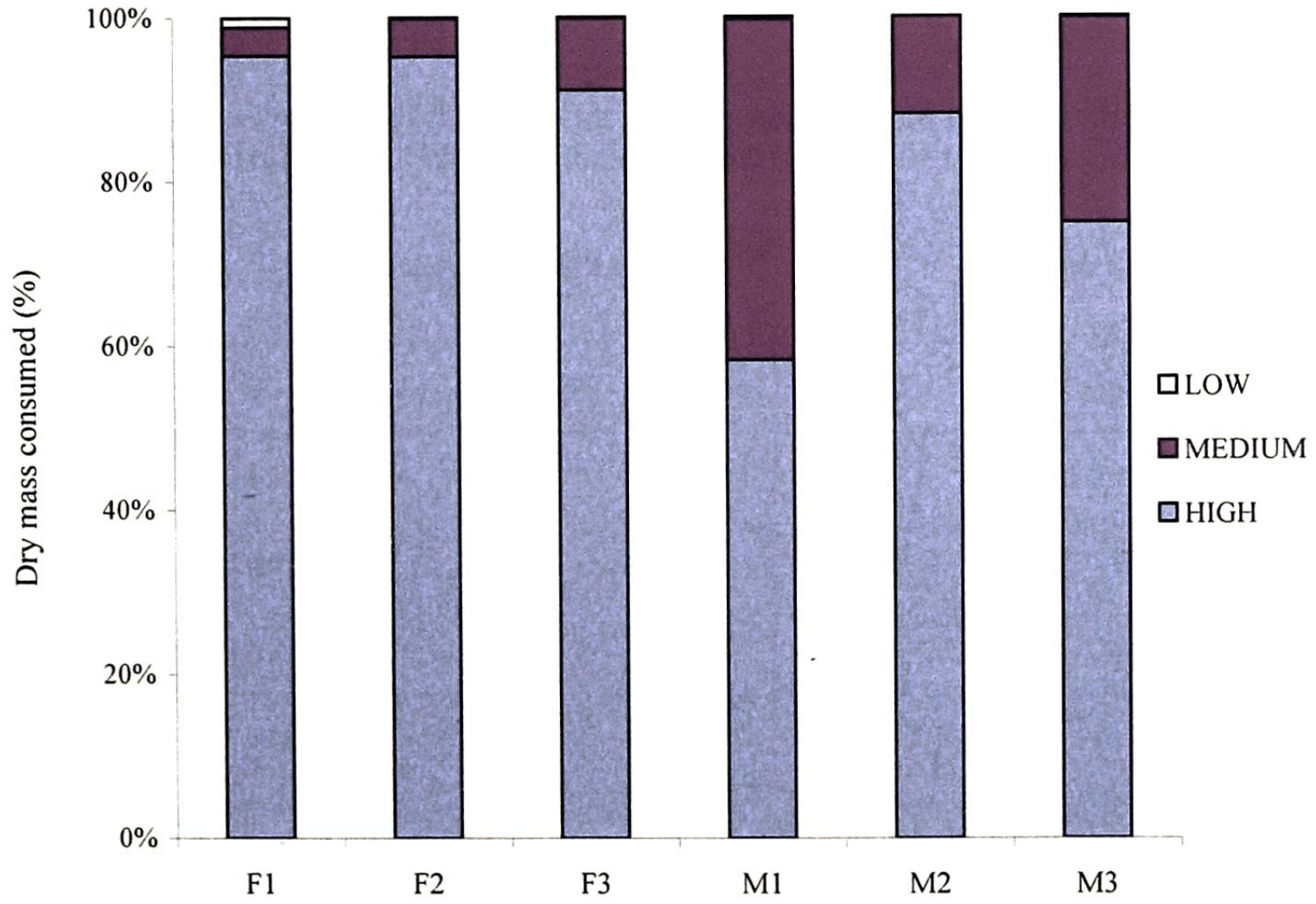


Figure 5.3. Mean consumption, expressed as percentages of mass in grams, of spinifex seeds in HIGH, MEDIUM, and LOW water content treatments. Each pie represents a different trial. *P. hermannsburgensis* = 9, *N. alexis* = 6.



P. hermannsburgensis



N. alexis

Figure 5.4. Consumption of spinifex seeds in relation to three different levels of water content in nine *P. hermannsburgensis* and six *N. alexis*. The percentage presented is the average over 5 repeated trials with the same animals. LOW, MEDIUM, and HIGH refer to the water content. F females, M males.

Table 5.2. Results of seed-water content selection trials for six *N. alexis* over five repeated trials. Values for Friedman two-way analysis of variance and Kendall's coefficient of concordance, degrees of freedom and *P* values are shown.

N. alexis	**Friedman's test statistic**	**Kendall's coefficient of concordance**	**df**	***P* values**
Trial 1	4.333	0.361	2	0.115
Trial 2	9.750	0.812	2	0.008
Trial 3	11.083	0.924	2	0.004
Trial 4	10.333	0.861	2	0.006
Trial 5	10.333	0.861	2	0.006

In the case of *N. alexis*, the lack of significance in trial 1 was due to a single individual that selected against seeds with the highest water content, choosing seeds in the MEDIUM first and then LOW treatments. No clear difference in consumption of seeds with different water content was shown between the sexes of both species (Table 5.3).

Table 5.3. Results of one-way ANOVA on the consumption of seeds in the three different treatments (HIGH, MEDIUM, LOW water content) in the two sexes of the two species.

	P. hermannsurgensis				***N. alexis***			
Water content	***F***	**df**	**Error df**	***P* values**	***F***	**df**	**Error df**	***P* values**
HIGH	0.644	1	7	0.449	0.767	1	4	0.431
MEDIUM	0.457	1	7	0.521	4.203	1	4	0.110
LOW	0.822	1	7	0.395	0.518	1	4	0.511

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5.4. Discussion

5.4.1. Water content selection trials

The results of the water content selection trials showed that the study rodents were capable of selecting seeds with the highest water content, and that their selection was consistent over repeated trials. Even though the water content levels offered to the mice are unlikely to resemble those encountered in the desert (see Chapter 6), these animals presumably experience selection to detect and select for the moistest seeds because of the scarcity of water in their environment. There was some individual variability in dry mass of seeds consumed in each treatment, but no obvious difference appeared between sexes; the ability to detect the moistest seeds is vital in deserts and presumably independent of sex. It would be interesting to test pregnant females to see if this ability is enhanced in such individuals. With regard to the MEDIUM and LOW treatments, seed selection was not apparent, perhaps because the difference between the two water contents was smaller. *Notomys alexis* consumed more seed in the MEDIUM treatments than *P. hermannsburgensis,* perhaps because, being bigger, individuals of this species simply needed more food. Despite this, none of the seeds in the HIGH, MEDIUM or LOW treatments was consumed completely during the trials. It is also possible that *N. alexis* consumed a high proportion of seed in the MEDIUM treatment, because they often fed at the end of the trial, when the difference in water content between treatments was reduced. In fact, the trials were run for twelve hours and the water content often varied during this time. According to this scenario, an important question is when the mice chose to forage, if at the beginning, in the middle or at the end of the night, and with what frequency. If foraging took place in pulses, mice could be faced with new ranges of water content each time.

From the general results it can be concluded that desert mice were able to differentiate differences of seed water content as small as 3% for *N. alexis*, and almost 5% for *P. hermannsburgensis*. Differences in discriminating ability are likely to exist amongst individuals. The rodents are likely to achieve discrimination by using olfaction to detect the water vapour emitted by seeds (Frank 1988b). If olfaction is the main cue used in detecting preformed water in seeds, variables such as soil moisture, air humidity, wind and presence of seed coat may play an important role in facilitating or compromising detection. Another method of differentiating moist from dry seeds may be their mass. Since rodents

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extensively handle seeds before eating, they may select seeds of highest mass for their size, even though this seems improbable (Frank 1988a). Taste and tactile cues may be equally important in the determination of water content (Frank 1988b).

If these results are compared with other studies on seed selection based on preformed water content using North American rodents (Reichman *et al.* 1986, Frank 1988a, b), it appears that the two species of Australian desert mice can better discriminate small differences in seed moistures; they can distinguish treatments separated by just 3-5% water content in comparison to 6.05% for their North American counterparts (Frank 1988b). This ability may have developed because these rodents, as most mammals, do not store excess water (Schmidt-Nielsen 1964, Frank 1988b). In contrast to North American rodents, Australian rodents do not cache seeds in highly humid burrows and thus cannot increase seed water content using the elevated hygroscopic power of seeds (Reichman *et al.* 1985, 1986, Frank 1988a). For this reason, Australian desert rodents are presumably under strong selection to detect the moistest seeds every time they feed. Moreover, if increased water loss occurs while foraging (Kotler *et al.* 1998) and water losses are incurred due to salivation during seed handling and husking (Vander Wall 1995a), it becomes imperative for these animals to maximise water intake to produce a positive water balance when choosing their food. These results also have implications for Model 1 of Chapter 4, because these rodents are not likely to be limited by free water.

5.4.2. Methodological problems

Despite the clear finding that *N. alexis* and *P. hermannsburgensis* detect and select for moist seeds, the findings of this chapter also revealed some difficulties when trying to experimentally reproduce different levels of water content in food. For example, while exactly the same procedures and equipment were used in seed preparation in all experiments, the final levels of water content produced in seeds were quite variable over both the pilot studies and water content selection trials. The use of colours also contributed to the variability. It is important to consider what the mice have been offered to clearly understand their selection. For this reason it was crucial to monitor seed samples for as long as possible during all procedures. Seed moisture contents are extremely susceptible to even minimal variations in humidity (Morton and MacMillen 1982). Are desert rodents so skilful as to be able to detect variations of 1% in the water content of their food? Such ability in detection may be unlikely (see examples in Heteromyidae, Frank 1988a, b). For

this reason, differences in selection arising from the use of colours may be minimal, but they must be acknowledged. Besides, biases accumulated via the processes of drying, sieving, weighing samples and collecting data could have contributed to the general noise of the results. Nevertheless, the findings clearly showed a general lack of selection for colours no matter which water content was involved in the trials, and seeds of the highest water content were consistently preferred by both species.

5.5. Conclusions

Pseudomys hermannsburgensis and *N. alexis* showed a strong ability to select for spinifex seeds containing high water content, with individual animals showing consistent selection over repeated trials. The ability to detect seeds with the highest water content is vital in animals that rely for most of their life cycle on water obtained from their food. In order to understand better the role of water and seeds in driving population dynamics of rodents in desert ecosystems, however, we need to clarify the selection pattern for preformed and metabolic water content in different types of seeds. As well as water, we need also to look at the importance of other constituents in seeds such as proteins, and energy content. Morphological characteristics, handling time and palatability of seeds can also be important in controlling the selection of different foods by desert mice. Seed-type selection is the subject of the next chapter.

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CHAPTER 6: SELECTION AND CHARACTERISTICS OF NATIVE SEED SPECIES

6.1. Introduction

Animals generally exhibit food preferences in their natural environment. Such preferences have been defined as the selection of one or more food types over a variety of other food types when all food types are equally available (Krebs 1989, Norbury and Sanson 1992). Food preference and consequent selection are extremely variable, even within the same species, and can depend on physiological, behavioural and morphological traits of individual animals as well as on external factors such as seasonality, environmental fluctuations, predation, competition and relative food availability.

According to optimal foraging theory (Pulliam 1974), foragers should select food that maximises net energy intake per unit time spent foraging. Moreover, they should evolve a certain degree of flexibility in the extent of their resource selection, becoming generalists when food is scarce, and specialists when food is abundant (Emlen 1966, MacArthur and Pianka 1966). Several studies have confirmed the predictions of this model (Smigel and Rosenzweig 1974, Richards 1983, Fantino and Abarca 1985, Hanson and Green 1989, Demott 1993, Illius and Gordon 1993). However, some authors disagree that maximising the net energy intake per unit time is the main pressure that animals respond to while foraging (Boyd and Goodyear 1971, Maynard Smith 1985, Gilbert and Owen 1990). Tenore (1977), White (1993, 2002), and Gutiérrez and Bozinovic (1998) separately identified nitrogen rather than energy as the limiting factor for individual success and the characteristic that most affects food preferences. The desert is very rich in plant forms, and all are rich in carbon-based structures and tissues. Energy, in the form of solar radiation, is certainly not limiting in deserts. Instead soil nutrients, in particular nitrogen, tend to be low in desert soils (Ellis and Lambrecht 1986, Morton 1985, Stafford Smith and Morton 1990) and consequently limiting to plants and animals. Estimates of the efficiency with which plants can fix energy, carbon and nitrogen, suggest that nitrogen is often the most limiting nutrient (West and Klemmedson 1978, Mattson 1980, Agren 1985), and White (1993) noted further that all plants and animals need sufficient nitrogen to grow and reproduce. Besides, population increases in deserts are often correlated with rainfall that induces production of green material and seeds in desert plants. Studies in North America have showed that the reproductive timing of rodents often coincides with the presence of green vegetation in the environment (Chew and Butterworth 1964, Beatley 1969, Batzli and

Pitelka 1971), and with its highest incidence in the diet of rodents (Batzli and Pitelka 1971, Bradley and Maurer 1971). For example, voles were induced to breed out of season by addition of green grass to their diet (Negus and Berger 1977). Allen and Hume (1997) showed the importance of green, unripe seeds, which are extremely rich in essential amino acids, compared to ripe seeds, in the diet of breeding desert birds. Nitrogen is usually dispersed at low concentrations, diluted by structural carbohydrates in senescing tissues, or locked away in the unpalatable, indigestible or even poisonous parts of plants (White 1993). To acquire this resource, large volumes of plant material have to be consumed, digested and absorbed by foragers with considerable expenditure of time and energy (White 1993). When plants respond to rain by growing new tissues and seeds, they mobilise nitrogen in forms that are more easily and readily absorbable by foragers at low cost (Sano and Kawashima 1982, White 1993, Rozan *et al.* 2001). Foragers should take advantage of the availability of such a limiting resource and synchronise their growth and reproduction within these narrow windows of abundance. Water is the other main limiting resource in deserts, as discussed in Chapter 5. According to these factors, desert rodents should select for seeds rich in nitrogen and water, and for which the cost of handling is minimum, in order to maximise their intake of key limiting nutrients.

When animals are foraging they are expected to maximise not just the rate of food (energy) intake but also the intake of the most limiting nutrients in their environment at that time. Depending on this constraint, they should vary their selection criteria. Numerous studies on rodents have tried to explain the selection criteria underlying food and especially seed selection. Omitting external pressures such as predation (Kotler 1984), and competition (Kerley 1991, Predavec 1997a), a long list of characteristics has been identified that affect the selection of seeds by rodents, and some of these findings are discordant and controversial, addressing different and opposite characteristics as to be the most important in the choice. Seed density (Smigel and Rosenzweig 1974), seed dispersion patterns (Price and Heinz 1984), seed size (Smith 1942, Brown and Lieberman 1973, Mares and Williams 1977, Price 1983a, Henderson 1990, but see also Smigel and Rosenzweig 1974), handling time (Kaufman and Collier 1981), free and metabolic water content (Schmidt-Nielsen *et al.* 1948, Morton and MacMillen 1982, Frank 1988a, b, Hulbert and MacMillen 1988, Murray and Dickman 1994b), energy and soluble carbohydrate content (Kelrick *et al.* 1986, but see also Jenkins 1988), rate of energy intake (Kerley and Erasmus 1991), energy (Reichman 1977, Vickery *et al.* 1994) protein to fibre ratio (Milton 1979, Gutiérrez and Bozinovic 1998), carbohydrates (Lockard and Lockard

1971), lipid content (Price 1983a), nitrogen content (Henderson 1990), and palatability (Emlen 1973, Hay and Fuller 1981, Kerley 1991) are some of the characteristics that rodents appear to select for. It seems clear that rodents exhibit variable patterns of seed choice, with preferences that change both temporally and spatially. It is also obvious that selection is rarely due to a single factor, because rodents are not faced with single units of nutrients but with complex mixtures of them. In addition, seeds have different shapes, sizes, coats and secondary mechanisms of defence (tannins, alkaloids, toxins etc.) that a forager has to handle in the shortest time possible (Mole and Waterman 1987, Henderson 1990, Siemens *et al*. 1992, Sundar Rao and Sino 1992, Cameron 1994). For these reasons the causes and factors underlying food preferences and selection can be multiple and extremely complex to understand. Laboratory trials enable the manipulation of food accessibility and abundance and the elimination of external factors. Hence, the issue of diet choice can be simplified to assess the components and characteristics of foods that lead to their selection.

Australian desert rodents exploit plant material and seeds to a large extent (Watts and Morton 1983, Murray and Dickman 1994a, Murray *et al*. 1999). The desert is rich in plant species that potentially constitute an invaluable source of food to rodents, especially in some seasons. The variability in seed characteristics is huge both in composition and morphology. Plant species also have a differential distribution both in time and among different microhabitats. Rodents are exposed to a great variety of seed types throughout the year, but also to a great variability in seed abundance. Rodents are likely to select particular characteristics of seeds depending on their dietary requirements and external constraints at the time of choice.

Murray and Dickman (1994a) found that *P. hermannsburgensis* and *N. alexis* consumed only nine seed species out of approximately thirty available at the time of sampling. This pattern can be explained by the rodents selection for some characteristics on some seed species. In another study on the same two species, Murray and Dickman (1994b) failed to find evidence for selection on the basis of four nutritional (water, nitrogen, energy, and dry matter) and two morphological (weight and linear size) characteristics, and they highlighted the large variability in individual preference within each species.

From the results of Chapter 4, the two rodent species showed apparently inconsistent selection of seed species in the field. In addition, the diets of the two study species were variable during different phases of their population cycles. The rodents might have been

selecting particular seed characteristics based on seed availability and physiological constraints of the population phases. Moreover, from the findings of Chapter 5 *P. hermannsburgensis* and *N. alexis* appeared very skilful in detecting moist spinifex seeds. Is a high content of free water a fundamental characteristic of seeds which rodents usually select for?

In order to understand more clearly the role of water and other seed nutrients in driving population dynamics, I tested the seed preferences of *P. hermannsburgensis* and *N. alexis* and compared their selection with seed constituents and morphology to explain the mechanisms that underlie such selection.

6.2. Materials and Methods

To determine the factors affecting the selection of seeds in desert rodents I offered a selection of thirty native seed species (Table 6.1) to the two rodent species, in a series of six separate trials. The term 'seed' will be used here to describe the functional dispersal and/or reproductive unit of a plant (diaspore), although some of the examined seeds are actually fruits (Reichman 1976). The experimental mice were maintained using the same husbandry procedures as during the trials of Chapter 5.

6.2.1. Description of the thirty native seed species analysed

All the seed species in the trials were collected from twelve trapping grids in the Simpson Desert, with most of the species obtained from Ethabuka site during four years of sampling (1998 to 2001). The species used in the trials represented usually the most common species available in the desert at the time, and comprise a broad spectrum of morpho-structural and nutritional variables. Moreover, most of them have been identified in previous dietary analyses of the diets of the two rodent species (McNaught 1994, Murray and Dickman 1994a, b, Chapter 4).

The floristic descriptions of the seeds used in the trials are presented in Table 6.1, and are derived from Jessop (1981) and Cunningham *et al.* (1981).

Table 6.1 Floristic descriptions of the seeds examined in the selection experiments. Characteristics are based on descriptions in Cunningham *et al.* (1981) and Jessop (1981).

Species	Family	Characteristics
Acacia dictyophleba	Mimosaceae	Perennial. Large shrub (up to 3 m). Seeds are similar in appearance to *A. cambagei*, but smaller.
Acacia georginae	Mimosaceae	Perennial. Small tree (up to 12 m). Large yellow seeds, laterally compressed and surrounded by a brown seed coat.
Aristida contorta	Poaceae	Annual or short-lived perennial grass to 30 cm high. Grains 3-4.5 cm long are contained in awns 3-7 cm long. The awns are slender, stiff, spreading. Outer husks pointed, purplish-black to dark-brown when young, straw-coloured when mature.
Cassia artemisioides	Caesalpiniaceae	Short-lived perennial shrub 1-2 m high. Two to twelve seeds are encased in a legume 4-8 cm long. They are 4 x 5 mm, obovate, dark greenish brown to nearly black, shining, flattish.
Cassia pleurocarpa	Caesalpiniaceae	Short-lived perennial shrub 1-3 m high. Seeds are triangular-shaped, 6 mm long, thick, dull, almost black, with a raised line across each.
Cleome viscosa	Capparidaceae	Erect annual forb, to 90 cm high. Seeds are numerous, blackish brown, transversely wrinkled, contained in a capsule 3-8 cm long, almost cylindrical, opening into two segments from the tip downwards.
Crotalaria cunninghamii	Fabaceae	Erect perennial subshrub (to 2 m). Seeds are yellow/orange and kidney-shaped, encased in a club-shaped pod, 4-5 cm long, swollen, hard, and velvety.
Dactyloctenium radulans	Poaceae	Short-lived semi-erect annual grass. Grains c. 1 mm long are obtusely trigonous, coarsely rugose, contained in spikelets 4-5 mm long.
Dicrastylis costelloi	Chloanthaceae	Shrub 45-90 cm high. Seeds are embedded in obovoid-globose, short-tomentose fruits, 3-3.3 mm diameter.
Dodonaea viscosa	Sapindaceae	Tall sticky hairless bushy shrub, 2-3 m high. Seeds are small and black/brown, encased in a green, red or purplish 3-4 winged membranous capsule. The capsule is 10-18 mm long and about as broad.
Enneapogon polyphyllus	Poaceae	Annual or short-lived perennial grass. Grains obovate-oblong, 1.5 mm long, encased in awns, 6-7 mm long, hairless except for a basal tuft of hairs and a row of sparse hairs just below the awns.
Eragrostis eriopoda	Poaceae	Perennial grass. Grains ovate, c. 0.8 mm long embedded in spikelets 6-22 mm long, 2-3 mm wide, straight or curved, green suffused with violet.
Eremophila macdonnellii	Myoporaceae	Shrub to 0.5 m high and broad. Seeds are large, rough surfaced and are encased in a papery grey seed coat.

Species	Family	Characteristics (continued)
Eriachne aristidea	Poaceae	Loosely or densely tufted annual or short-lived perennial grass, 8-45 cm high. Grains are cuneate to obovate, laterally compressed, plano-convex, 3-3.5 mm long, encased in bifid awns.
Eucalyptus pachyphylla	Myrtaceae	Dense tree 1-4 m high. Seeds are encased in hemispherical fruits, strongly ribbed, woody 1.5-1.7 x 2-3 cm. Seeds are irregularly broad-lunate, edges flattened and wing-like, faint reticulate, red-grey-brown.
Fimbristylis dichotoma	Cyperaceae	Slender tufted perennial sedge. Nuts are biconvex, trabeculate, reddish-brown, 0.8-1 x 0.6-0.7 mm.
Goodenia cycloptera	Goodeniaceae	Downy or hairy perennial forb with long spreading or erect stems 40-50 cm long. A globular capsule, 6-8 mm diameter, contains 6-8 flat almost round black seeds. Each seed is surrounded by a thick broad wing.
Grevillea stenobotrya	Proteaceae	Erect or spreading shrub, to about 4 m high. Seeds are laterally compressed and elliptic, with a woody seed coat surrounded by a membranous wing. They are encased in a hard rounded flattened capsule about 12 mm across, with a short recurved beak.
Newcastelia spodiotricha	Chloanthaceae	Small shrub (1-2 m). Seeds are round and woody, protected by a velvety, easily removable beige seed coat (2.5-3 mm diameter).
Oldenlandia pterospora	Rubiaceae	Erect, branched perennial. Few small blackish- brown seeds encased in capsules that open in two valves.
Othonna (*Senecio*) *gregorii*	Asteraceae	Erect hairless blue-green annual forb, 10-30 cm high. Seeds are slender-cylindrical, 5-8 mm long, usually densely silky, rarely hairless.
Paractaeneum (*Plagiosetum*) *refractum*	Poaceae	Leafy tufted annual or short-lived perennial grass, to 50 cm high. Grains are oblong, encased in an oblong-elliptic floret, apiculate, 4.5-5 mm long.
Ptilotus polystachyus	Amaranthaceae	Green herbaceous ephemeral or perennial forb to 1.5 m tall. Seeds covered by a membranous seed coat at the base of long, tufted ovaries.
Sclerolaena (*Bassia*) *bicornis*	Chenopodiaceae	Erect shrub to 60 cm in height and diameter, with white-woolly branches. Seeds are embedded in a fruiting body, woody, more or less globular, 7-8 mm diameter, enveloped in white wool, with two sharp, stout, rigid spines.
Stylobasium spathulatum	Stylobasidaceae	Erect medium sized bush to 2 m. Drupes are globular, c. 12 mm diameter, covered in a papery brown coat, surmounted by an expanded calyx.
Trachymene glaucifolia	Apiaceae	Erect annual or probably biennial forb, to 80 cm high. Seeds are flat and circular contained within a thin brown seed coat, covered with numerous slender protuberances on each face.

Species	Family	Characteristics (continued)
Tragus australianus	Poaceae	Small ascending or erect annual grass, 10-40 cm high. Grains are more or less fusiform, 1.5-2 mm long, contained inside spikelets, burr-like from the dense cover of short hooked spines.
Trianthema pilosa	Aizoaceae	Prostrate annual forb with branches to 40 cm long, papillose. Two flat, black wrinkled seeds are embedded in a fruit truncate and centrally depressed.
Trichodesma zeylanicum	Boraginaceae	Stiff, woody, grey-hairy erect annual or perennial forb, about 1 m high. Four seeds composed a nutlet. Each nutlet is usually smooth mottled on the outer face and with minute tubercles on the inner face.
Triodia basedowii	Poaceae	Perennial grass forming compact or irregularly-shaped tussocks to 40 cm high and 75 cm wide. Small whitish beige seeds are encased in florets 6-8 mm long with three broad lobes at the tip.

6.2.2. Pilot study on cafeteria versus mixed trials

Nine *P. hermannsburgensis* were used in a pilot study with five seed species to compare a cafeteria-style trial with an trial in which the seeds were mixed together. In the cafeteria trial the five seed species were offered to the mice overnight in five separate plastic containers, which were distributed randomly in a large, sand-filled glass tank. Because seed consumption was assessed by weighing, a control container of seeds was used to correct for water gain or loss during the night. At the end of the trial the seeds were collected, the sand sieved and the amount in grams of each seed species consumed was calculated (after correction for water evaporation or absorption). These results were then compared with those from a second trial where the same seed species had been presented to test animals after mixing them together. The Wilcoxon signed ranks test (Siegel 1956, Quinn and Keough 2002) was used to compare consumption in both trials. After examining the results, I decided to use mixed seed trials to better mimic seed availability in desert depressions, and therefore the situation most likely to occur in the rodents' natural habitat.

6.2.3. Seed selection trials

A total of nine *P. hermannsburgensis* was used in trial 1. In trial 2, the number was reduced to eight due to death of an individual. The number was further reduced to seven for trials 3 to 7 after another individual died. The number of *N. alexis* in each trial was six. These individuals had been used previously in trials to determine selection of water content in seeds (Chapter 5). During each trial a total of five seed species were tested together, with the exception of trial 2, where only four species were offered, and trial 6, where six species were offered. These differences were due to a temporary lack of available seeds. The thirty species were not offered all together in a single trial to avoid biases and difficulties in separating them after the trial. Moreover, previous studies have shown that using too many species makes the interpretation of seed choice extremely complex (Murray and Dickman 1997). Species were chosen to avoid mixing seeds that were morphologically very similar to each other. Different amounts of each seed species (0.3 to 3 g), due to different availability, were mixed together and offered with their husks intact in three different plastic dishes (10 cm diameter x 6 cm deep), randomly distributed to mimic desert depressions in the same large, sand-filled glass aquaria used in Chapter 5. Each species was only trialed once. Plastic dish positions were re-randomised amongst

trials to prevent any possible amongst-trial learning. One control was used to monitor eventual water loss or gain during the trial, as in the pilot study. Mice were allowed to forage singly overnight. The time span between trials was a minimum of three nights. At the end of the trials the mice were removed from the experimental tank, and the sand sifted to collect uneaten seeds. Seeds were then sorted to species and weighed. No seed species was ever completely depleted during the run of the trials. Initial and final masses of the seeds were recorded. The mass of each seed species consumed was corrected for water loss or gain following the formula of Chapter 5 (see Materials and Methods), and standardised according to the initial mass offered. The mean amounts of each seed species eaten were calculated in each trial, and standardised further by the basal metabolic rates (BMR) of the two species to compare corrected seed consumption. The mean masses of the experimental mice were used in the calculation of BMR by entering them into the equation in McNab (1988) for desert seed-eaters. After calculations, the values of consumption for *P. hermannsburgensis* were converted by multiplying by a factor of 0.9178, resulting from the division of the BMR of *N. alexis* (1.1623 cm3 O_2 g^{-1} h^{-1}) by the BMR of *P. hermannsburgensis* (1.2665 cm^3 O_2 g^{-1} h^{-1}), where O_2 is oxygen uptake, g is mass in grams and h hours.

Finally, the mean amount of the thirty species consumed in each trial was ranked (1 the most preferred species, n the least), and the twelve most selected species together with *Eragrostis eriopoda* were offered together to the two rodent species in trial 7, following the same procedure described above. *Eragrostis eriopoda* was included in the final trial because a careful examination of the spikelets of this species offered in the previous trial revealed that the samples used did not contain seed grains. The new samples used in the final trial contained seeds.

6.2.3.1. Analyses

The consumption of each seed species by the two rodent species in each trial was compared with one-way ANOVAs to detect interspecific differences in amounts consumed.

Friedman's test and Kendall's coefficient of concordance were used to test for concordance in preference for seed species. Mantel's test (Mantel 1967, Luo and Fox 1994, Sokal and Rohlf 1995, Liedloff 1999) was used to compare the overall interspecific concordance in preference in each trial. This test compares a distance or similarity matrix

with an hypothesis matrix to determine if the two matrices are significantly correlated. In this study, the matrix of consumption of seed species by one rodent species was compared with the matrix of consumption of the same seed species by the other rodent species for each trial, under the null hypothesis that there was no association between elements in dissimilarity matrix 1 and dissimilarity matrix 2. If the value for the test, g, was associated with a probability level of 0.05 or less, the null hypothesis was rejected. Data on consumption were log-transformed and the Euclidean distance was chosen as the measure of similarity because it was based on continuous data.

Total mean seed consumption + standard deviation in each trial was calculated. The percentage of seed eaten of the total amount offered was also plotted for each trial for the two species. A comparison of the difference of mean total consumption amongst trials was performed using a Wilcoxon signed ranks test. Because multiple comparisons were made of the same data, it was appropriate to reduce the probability of committing type-1 errors. Hence, if a probability of <0.05 was found, it was readjusted using sequential Bonferroni correction (Quinn and Keough 2002).

After transformations to improve normality and homogeneity of variances, one-way ANOVAs were again used to compare the total mean seed consumption of the two rodent species in each trial. One-way ANOVAs were also used to detect any differences between the two sexes of each species in their total consumption of seed in each trial.

To examine whether the number of presented seed species affected the selection process, the consumption of the thirteen seed species of trial 7 was compared with the consumption of the same thirteen species in the separate trials using a Wilcoxon signed ranks test.

6.2.3.2. Indices of preferences

Four indices of preference were calculated for comparison purposes. First, the amount consumed of each seed eaten in the overnight trials was used as an indication of relative preference for that particular species. The second measure of preference used was Manly's alpha (Manly *et al*. 1972, Manly 1974). This method allows for the exploitation of prey during an trial, by taking into account the proportions of the different food categories consumed during a trial (Cock 1978). According to Manly (1974), if selected prey are not replaced during the trial, then the model to use is a Type Two Selection Model. A value of alpha was calculated for each seed species using the formula presented by the authors

(Manly *et al.* 1972, Manly 1974), then ranked according to this value. Because Manly's alpha is more suitable for non-continuous data, for equally abundant prey items and for N≥10, a further index of preference was used in this study, which was potentially more appropriate to the data available. Vanderploeg and Scavia's Normalized Selectivity Coefficient, which accounts for various proportions of prey available, was used in conjunction with Vanderploeg and Scavia's Relativised Electivity Coefficient (Vanderploeg and Scavia 1979a, b, Lechowicz 1982). The Normalised Selectivity Coefficient represents "the feeder's perception of the value of a food item in relation to both its abundance and the other food types available" (Lechowicz 1982). The equation used to calculate the Normalised Selectivity Coefficient (W_i) is the following:

$$W_i = \frac{(X_i - R_i)/X_i}{\sum_i (X_i - R_i)/X_i}$$

where X_i is the amount of food item *i* offered at the onset of the trial, and R_i is the amount of food item *i* left at the end of the trial.

The expected value for random feeding is a function of the number of food items: 1/n, where n is the number of food types in the trial. This index varies between 0 and 1, with values above 1/n indicating preference and values below 1/n indicating avoidance.

The Relativised Electivity Index (E_i) is based on the Selectivity Coefficient, W_i, and the number of available food items. This index has the advantage of varying between –1 (maximum avoidance) and +1 (maximum preference), with the zero value representing random feeding. Moreover, it includes a measure of the deviation from random feeding that can be useful in comparisons, even though Lechowicz (1982) recommended limiting direct comparisons of electivities to samples with the same food items. The equation of the Relativised Electivity Index is the following:

$$E_i = \frac{[W_i - (1/n)]}{[W_i + (1/n)]}$$

where W_i is the value of the Normalised Selectivity Coefficient, and n is the number of different food items used in the trial.

Finally, the values of each index of preference obtained for each seed species in each trial were ranked, assigning 1 to the most preferred species and n to the least. Comparison of ranks of each of the four preference indices showed them to be almost identical. After examining the distribution of these indices, the mean ranks were chosen and used in the remaining analyses.

6.2.4. Seed characteristics

During the course of this study some nutritional and morphological characteristics of native seed species were analysed and reviewed. Sixty-one native seed species were examined. Appendix 16 (Table 14) presents data on the whole set of native seed species extracted from different sources, with their characteristics, means and standard deviations shown when available. The characteristics measured with different procedures were standardised for comparisons.

Data for some of these species were collected from tables in Latz (1996), Brand Miller *et al.* (1993), and McNaught (1994). The remaining species were analysed during this study. The species on Latz's table (*Acacia dictyophleba*, *Calandrinia balonensis*, *Eragrostis eriopoda*, *Eucalyptus gamophylla*, *Fimbristylis oxystachya*, *Stylobasium spathulatum*) were analysed for protein (g/100 g), free water content (g/100 g), fat (g/100 g), ash (g/100 g), carbohydrate (g/100 g), energy (kJ), sodium, potassium and calcium (mg/100 g). Brand Miller *et al.* (1993) examined energy (kJ), free water content (g), protein (g), fat (g), carbohydrate (g), dietary fibre (g), ash (g), vitamin C (mg), sodium, potassium, magnesium, calcium, iron, zinc and copper (mg) of *Acacia dictyophleba*, *Acacia ligulata*, *Acacia longifolia*, *Calandrinia balonensis*, *Eragrostis eriopoda*, *Eucalyptus gamophylla*, *Fimbristylis oxystachya*, *Portulaca intraterranea*, and *Stylobasium spathulatum*. McNaught (1994) analysed forty-four native seed species, measuring largest linear dimension (LLD in mm), mass (air-dry in mg), free water content (%), and hardness (see methodology of McNaught 1994). I measured Carbon, Hydrogen and Nitrogen in twenty-one desert seed species collected in the study site in 1999. Seed samples were analysed by the Dumas total combustion method using an elemental analyser (CHN-1000, Leco Inc., St Joseph, MI) to determine the percentage seed carbon (Carbon), hydrogen (Hydrogen), and nitrogen (Nitrogen). In addition to these analyses, thirty native species, the same offered during trials to mice, were collected from the study site during a period of three years 1999-2001 and maintained in sealed plastic bags. I measured a series of nutritional and morphological characteristics of these seeds. Seeds were first dried and ground when necessary for the analysis. As a result of this procedure different variables were available and measured for different species.

1. Energy (kJ/g): was measured by bomb calorimetry using a Gallenkamp autobomb automatic adiabatic bomb calorimeter (Gorecki 1975), on dry, ground seeds (n=3), using 0.100 to 0.350 g of seed in each analysis.

2. Ash (g): was measured weighing the remains in the crucible after the combustion of the seeds (n=3).
3. Nitrogen content and crude protein (%): were determined in duplicate for ground seeds (n=2 for each seed species) by the Kjeldahl method for nitrogen (Clare & Stephenson 1964, Ivan *et al.* 1974). Crude protein was calculated by multiplying nitrogen concentration by 6.25.
4. Free water content (g): was calculated by drying ground seeds at 70° C for three days to a constant mass (n=3) and expressed as the proportion of mass loss of the original air-dry mass.
5. Dry matter (g): was determined by weighing the original air-dry sample after free water had been removed.
6. Largest Linear Dimension (LLD, mm): was expressed as the mean and standard deviation of the longest dimension of fifteen seeds of the same species.
7. Mass (mg): was expressed as the mean and standard deviation of the air-dry mass of fifteen seeds of the same species.
8. Hardness (index): was expressed as an index. This index reports the mass under which the seed coat breaks. The seed was positioned under a device with a pointed tip joined to a platform upon which different masses were applied. The seed was observed under a microscope to record the exact point-break.

Most of the species were analysed initially with their awns, seed coats or husks intact.

In order to assess the part of the seed that rodents usually eat (Jenkins 1988), the kernels of the thirteen species offered in trial 7 were analysed when possible, after removing the husk and other not-ingested parts of the diaspores. For each of these seed species another two morpho-structural characteristics were measured.

9. Ratio of kernel to husk of the largest linear dimension of the entire seed (LLD % E/H,): the longest dimension of the entire, intact seed and embryo/endosperm were measured in order to establish the relative size of the portion ingested by mice (n=15). The relative dimension of Embryo/Endosperm of the entire seed was expressed as a percentage.
10. Ratio of kernel to husk of the entire air-dry seed mass (m % E/H,): husk and embryo/endosperm were weighed in order to assess the relative mass of the portion ingested by mice (n=15). The proportion of Embryo/Endosperm of the entire seed was expressed as a percentage.

Finally, I measured one aspect of the behaviour of the two rodent species when they encountered seeds.

11. Handling time (*N. alexis* handling time, *N.*h.t. (s), and *P. hermannsburgensis*, *P.*h.t. (s)): using a hand-held stopwatch was measured the period elapsed between the pick-up of a seed from the ground and the discard of the remains of the seed after an animal had processed it by husking and chewing. Twenty-seven native seed species were offered intact to nine *P. hermannsburgensis* and six *N. alexis* and the mean and standard deviation handling time calculated when possible (n=5). Some seeds were untouched by the rodents. Food was removed 24 hours before these trials. *Notomys alexis*, because of their characteristic shyness, were more difficult to time and just five animals gave analysable results. Pearson product-moment correlation coefficients and *t*-tests (Sokal and Rohlf 1995) were used to compare handling times for the two species.

6.2.5. Regression analyses

For each species of rodent the relationships between seed consumption and seed nutritional and morpho-structural characteristics were investigated by regression analyses. Initially the mean consumption and the various indices of each tested seed were checked for normality, linearity and homogeneity against each of the nutritional and structural characteristics using simple linear regressions. Analysis of scatterplots, residuals and boxplots suggested transforming each variable to improve linearity, homogeneity and nomality. Variables expressed as proportions or percentages were arcsine-transformed, the remaining variables were log-transformed (Quinn and Keough 2002). Multiple regressions were run of the mean preference ranks and the seed nutritional and morpho-structural variables, choosing manually all the possible combinations amongst variables. Correlation matrices were run of seed nutritional and morpho-structural variables for each trial. Where high correlations were observed between pairs of variables, the two variables were not included in the same model of predictors (Quinn and Keough 2002). Moreover, tolerances for each model produced were checked to avoid collinearity (Quinn and Keough 2002). Considering the nature of the data and the low number of observations for most of the trials, stepwise multiple linear regressions were regarded as being non-precise and potentially yielding arbitrary results (James and McCulloch 1990, Quinn and Keough 2002). If more than one feasible model was obtained for each trial, the best fit was

therefore determined using the Akaike Information Criterion (AIC) (Akaike 1978, Quinn and Keough 2002). This criterion selects a model on the basis of the number of predictors, the number of observations, and the sum of squares of the residuals. The equation is the following:

$$AIC = n[\ln(SS_{Residual})] + 2(p + 1) - n\ln(n)$$

where n is the number of observations, p is the number of predictors in the model, and $SS_{Residual}$ is the sum of squares of the residuals.

6.2.6. NIRS Analysis

Twenty-seven of the above-described seed species were analysed using near infrared reflectance spectroscopy (NIRS Analysis) (Shenk *et al.* 1992, Foley *et al.* 1998), in an attempt to further clarify factors underlying seed selection by the two rodent species. This analysis depends on the number and type of C-H, N-H, and O-H bonds in the material being analysed. A predictive statistical model is used to combine the spectral features resulting from the analysis with reference to compositional or functional analyses of the material. The model so obtained is used to predict the composition of the sample (Foley *et al.* 1998).

Due to the nature of the samples, which represented a very heterogeneous range of particle sizes (Casler and Shenk 1985, Windham 1987), the analysis did not produce any interpretable results, and no pattern was observed (R^2 was highly variable within the two groups). For this reason this analysis and its results have been omitted from the rest of this chapter as uninformative.

6.3. Results

6.3.1. Characteristics of the thirty native seed species analysed

Table 6.2 presents the studied species and their characteristics. E indicates the seed species for which only the kernel was analysed without husks and seed coat. The seed species tested appeared very diverse in their morpho-structural and nutritional characteristics. Handling times of the two species were highly correlated (r=0.942,

Table 6.2. Seed species tested and their nutritional and morpho-structural characteristics. For abbreviations see the text. E indicates the seed species for which only the kernel was analysed without husks and seed coat.

Species	Ash (g)	Energy kJ/g	Water (g)	Dry Matter (g)	Protein (%)	C (g)	H (g)	N (g)	LLD (mm)	LLDEH (%)	Mass (mg)	mEH (%)	Hardness	*N*.h.t. (s)	*P*.h.t. (s)
Acacia dictyophleba E	0.03	13.68	0.07	0.93	23.70				4.19		10.37			21.0	25.0
Acacia georginae E	0.01	22.02	0.07	0.93	39.12				8.89		86.20				
Aristida contorta E	0.01	19.67	0.08	0.92	32.64				9.06	6.86	1.58	29.40	0.07	5.8	11.1
Cassia artemisioides E	0.04	19.41	0.07	0.93	18.32	0.40	0.06	0.03	6.10		20.30		0.04		
Cassia pleurocarpa E	0.03	19.98	0.06	0.92	20.12				6.10		27.00		0.04	33.0	68.0
Cleome viscosa	0.01	23.98	0.05	0.95	15.46				1.13		0.92			10.0	7.0
Crotalaria cunninghamii E	0.03	19.19	0.34	0.66	27.37				5.97		55.00		0.09		
Dactyloctenium radulans E	0.01	17.73	0.08	0.92	20.65				1.03		0.29				
Dicrastylis costelloi	0.08	21.44	0.05	0.95	3.65	0.49	0.06	0.00	4.10		20.30		0.13	40.0	56.0
Dodonaea viscosa E	0.01	25.29	0.04	0.96	32.21				3.41	65.77	17.50	42.60	0.09	10.1	28.7
Enneapogon polyphyllus E	0.01	20.02	0.07	0.93	34.92				2.64		3.40				
Eragrostis eriopoda E	0.01	18.02	0.07	0.93	15.55				0.88	46.54	0.14	11.99	0.29	3.5	3.4
Eremophila macdonnellii E	0.02	25.30	0.03	0.97	29.22				11.66		291.00		0.28	2.2	2.7
Eriachne aristidea E	0.01	18.81	0.07	0.93	20.22				4.81	15.09	2.18	19.50	0.43	4.5	7.4
Eucalyptus pachyphylla E	0.02	21.93	0.05	0.95	27.35				2.68	100	1.63	77.90		3.5	8.5
Fimbristylis dichotoma E	0.20	11.08	0.11	0.95	11.00				1.08		0.21				
Goodenia cycloptera	0.02	24.79	0.06	0.94	16.23				5.48	85.61	1.25	68.73	0.27	21.8	22.0
Grevillea stenobotrya E	0.06	29.43	0.04	0.96	31.80	0.52	0.07	0.03	12.58	60.38	23.30	62.85	0.58	24.7	58.1
Newcastelia spodiotricha E	0.01	20.86	0.06	0.94	3.06				6.80		8.35				
Oldenlandia pterospora E	0.06	22.52	0.06	0.94	14.34				1.24	100	0.22	100		1.7	3.8
Othonna gregorii	0.01	20.83	0.06	0.94	19.05				22.60		4.11				
Paractaeneum refractum E	0.01	19.37	0.07	0.93	24.54				4.66	11.75	4.18	16.42	0.41	3.6	9.0
Ptilotus polystachyus E	0.02	20.07	0.08	0.92	26.59				10.90	10.13	3.40	18.21	0.49	10.2	15.3
Sclerolaena bicornis E	0.01	19.08	0.05	0.95	27.05				5.37		59.50				
Stylobasium spathulatum E	0.02	5.15	0.01	0.96	12.30				7.14		168.00				
Trachymene glaucifolia E	0.02	23.03	0.07	0.93	12.40	0.49	0.07	0.02	5.76		1.36		0.13	19.0	33.0
Tragus australianus E	0.01	17.21	0.07	0.93	20.95				3.84	25.44	0.87	6.95		3.2	4.4
Trianthema pilosa E	0.03	22.23	0.07	0.93	16.92				6.94		5.77				
Trichodesma zeylanicum E	0.01	27.75	0.03	0.97	27.72				3.69	69.62	7.80	49.68	0.63	8.7	23.4
Triodia basedowii E	0.02	18.08	0.08	0.92	21.38	0.40	0.07	0.03	2.45	16.87	1.69	8.27	0.11	10.1	8.4

$P<0.001$), and very similar (t-values ranged from –2.460, df= 13.8 to 2.071 df=5.3, $P>0.05$ in all cases).

Table 6.3 presents the variables measured in each trial.

Table 6.3. Morphological and nutritional characteristics measured in thirty native seed species during seven trials. Xs indicate the characteristics recorded for each trial. See text for explanation of abbreviations.

Tr. #	Ash	Energy	Water	Dry Matter	Protein	C	H	N	LLD	LLD E/H	Mass	m E/H	*N*.h.t.	*P*.h.t.	Hardness
1	x	x	x	x	x	x	x	x	x		x				x
2	x	x	x	x	x				x		x		x	x	
3	x	x	x	x	x				x		x				
4	x	x	x	x	x				x		x				
5	x	x	x	x	x				x		x				
6	x	x	x	x	x				x		x				
7	x	x	x	x	x				x	x	x	x	x	x	

6.3.2. Pilot study on cafeteria versus mixed trials

The results of the pilot study to test differences between cafeteria and mixed seed trials showed that only *Dicrastylis costelloi* was consumed more in cafeteria than in mixed seed trials (Z=-2.67, $P<0.01$). Biases in the separation of the seeds after the trials may help to explain this difference. There was no difference in the consumption of *T. basedowii*, *C. artemisioides*, *G. stenobotrya*, and *T. glaucifolia* between cafeteria and mixed seed trials. No many seeds were found in the sand when it was sieved.

6.3.3. Seed selection trials

In the seven selection trials, the two rodent species showed selection for some species and avoidance of others. Within the same rodent species, a quite consistent concordance in seed choice was shown amongst individuals. Tables 6.4 and 6.5 show the results of the Friedman's and Kendall's coefficient of concordance tests within each rodent species.

Table 6.4. Results of seed selection trials for seven *P. hermannsburgensis* over seven trials. Values for Friedman two-way analysis of variance and Kendall's coefficient of concordance, degrees of freedom and *P* values are shown.

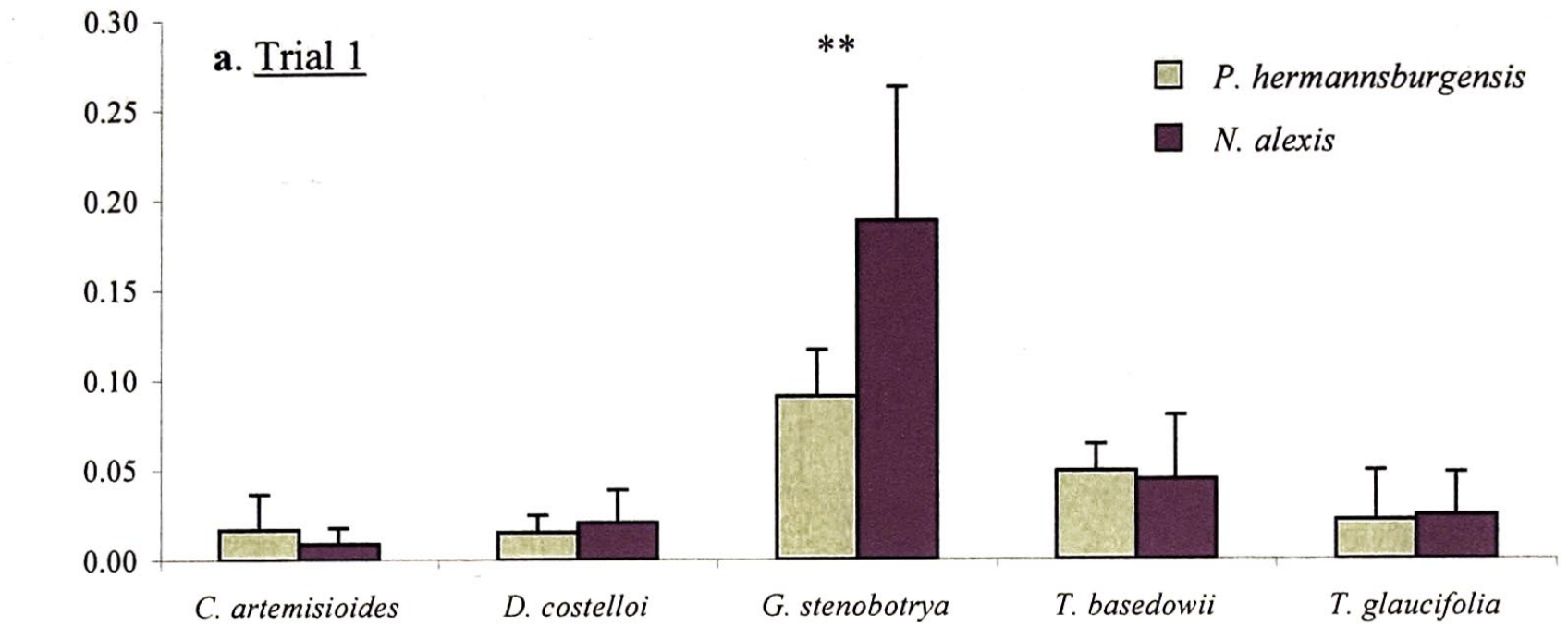
P. hermannsburgensis	**Friedman's test statistic**	**Kendall's coefficient of concordance**	**df**	***P* values**
Trial 1	23.156	0.643	4	< 0.001
Trial 2	13.050	0.544	3	0.005
Trial 3	22.743	0.812	4	< 0.001
Trial 4	24.200	0.864	4	< 0.001
Trial 5	21.400	0.764	4	< 0.001
Trial 6	29.367	0.839	5	< 0.001
Trial 7	64.823	0.772	12	< 0.001

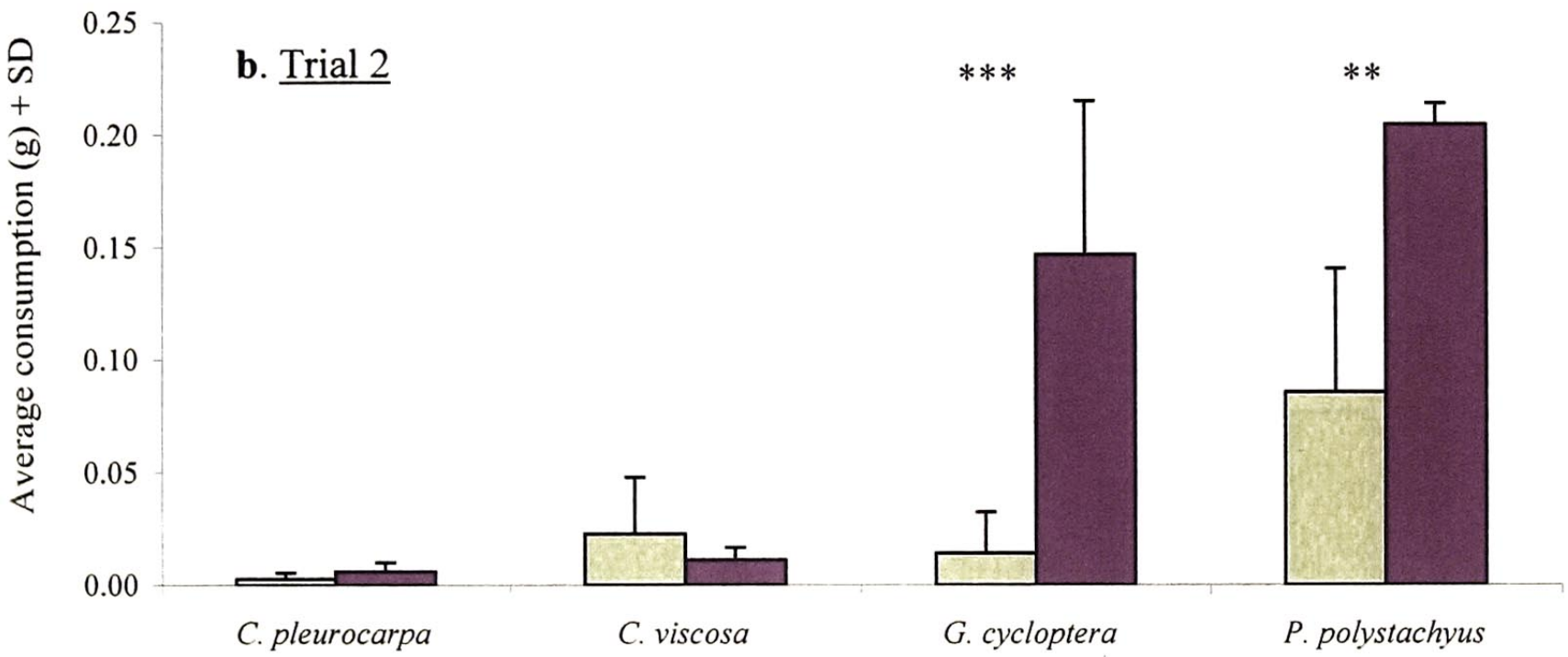
Table 6.5. Results of seed selection trials for six *N. alexis* over seven trials. Values for Friedman two-way analysis of variance and Kendall's coefficient of concordance, degrees of freedom and *P* values are shown.

N. alexis	**Friedman's test statistic**	**Kendall's Coefficient of Concordance**	**df**	***P* values**
Trial 1	14.267	0.594	4	0.006
Trial 2	16.000	0.889	3	0.001
Trial 3	19.733	0.822	4	0.001
Trial 4	15.967	0.665	4	0.003
Trial 5	18.800	0.783	4	0.001
Trial 6	27.119	0.904	5	<0.001
Trial 7	44.412	0.617	12	<0.001

In trial 2 *P. hermannsburgensis* showed weaker concordance, while in the remaining trials all individuals appeared to select native seeds with considerable agreement, even when the number of seed species was higher and the variety elevated as in the trial 7. In the case of *N. alexis*, only trial 1 failed to show very strong agreement between mice, although concordance amongst individuals was also not striking in trial 7, where the larger variety of seed species created slightly more divergence in seed selection.

Little difference was detected in the selection of the thirty native seed species between the two species. In trial 1 (Figure 6.1**a**) *N. alexis* consumed more *Grevillea stenobotrya* seed than *P. hermannsburgensis*. In trial 2 (Figure 6.1**b**) a similar pattern for the two seed species *Goodenia cycloptera* and *Ptilotus polystachyus* was observed. *Paractaeneum refractum* was consumed significantly more by *N. alexis* than *P. hermannsburgensis* in





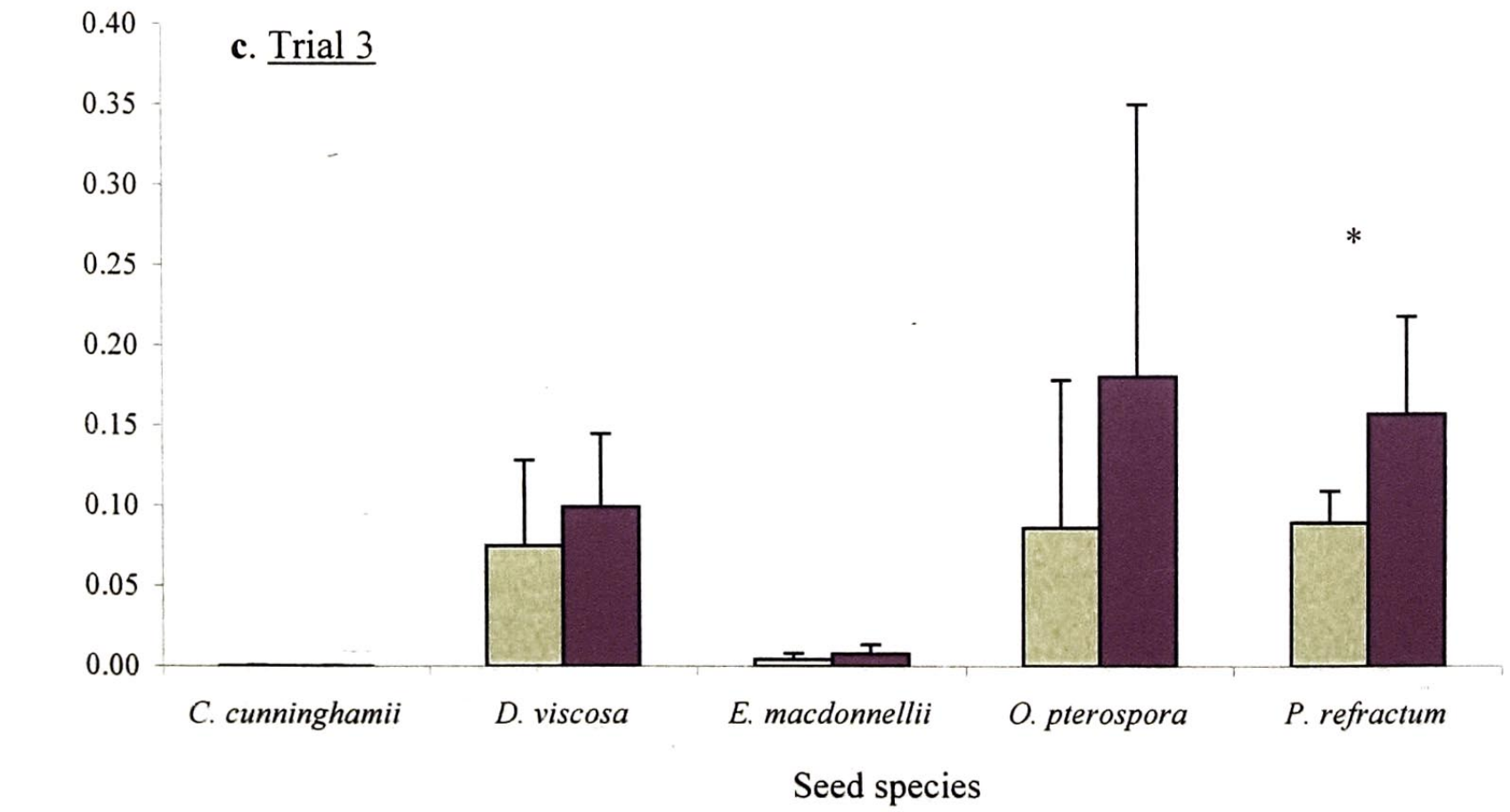
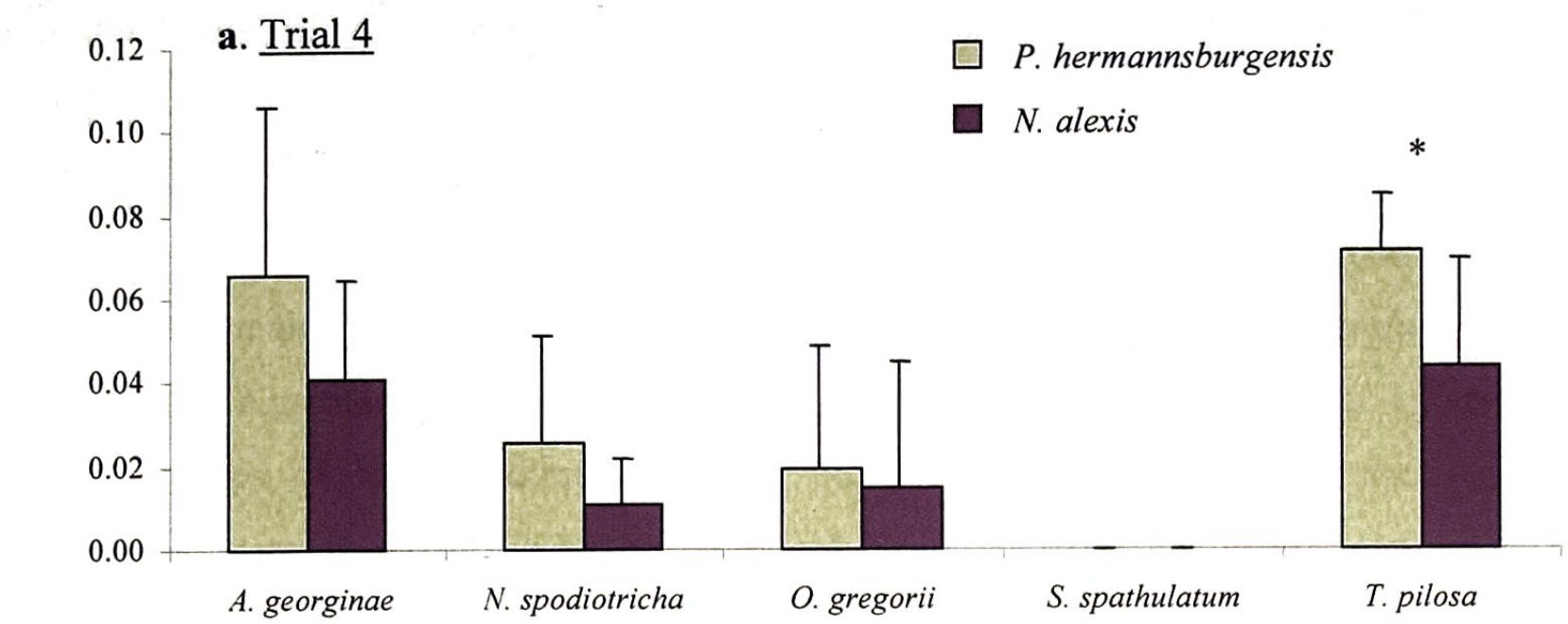
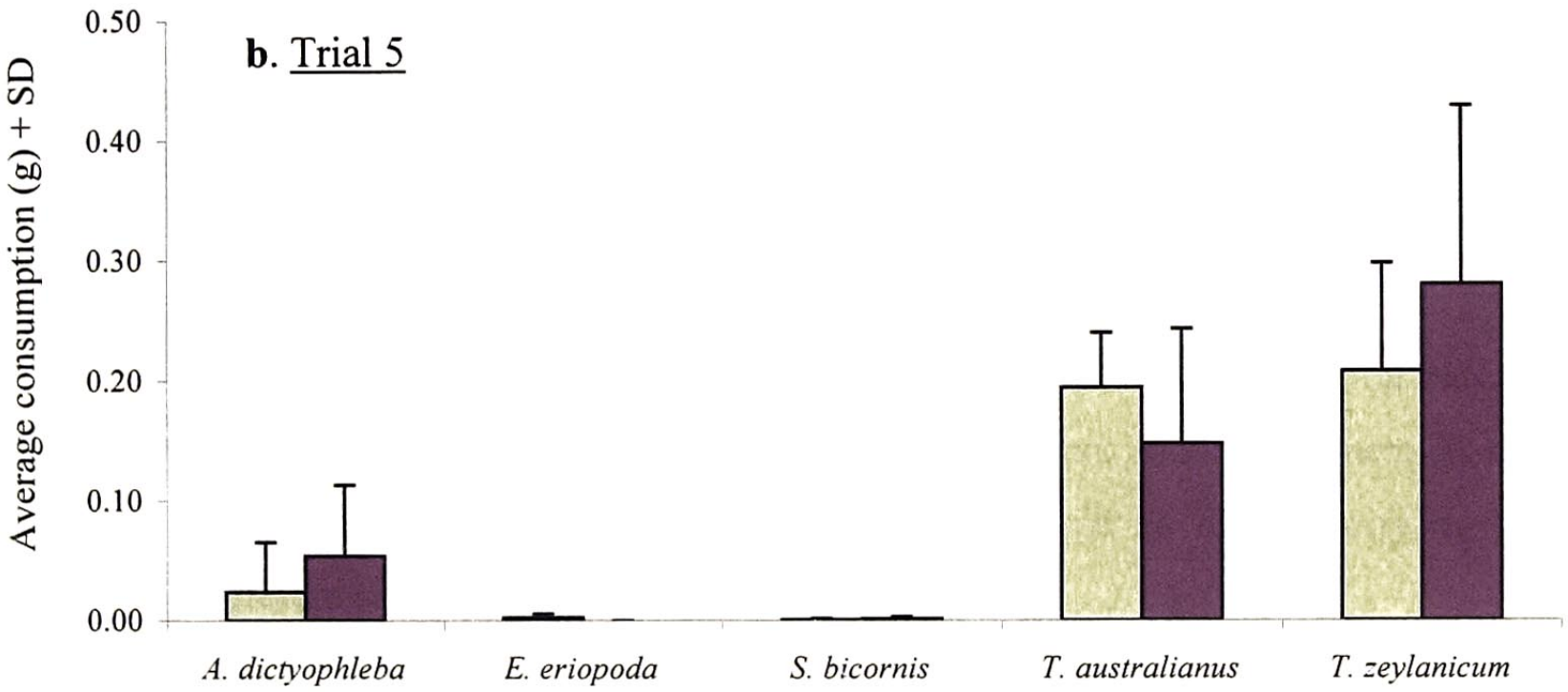


Figure 6.1 **a**, **b**, **c**. Average seed consumption corrected by BMR (Basal Metabolic Rate) + SD of the two rodent species in trial 1 (**a**), 2 (**b**), and 3 (**c**). In trial 1 *P. hermannsburgensis* n=9, *N. alexis* n=6. In trial 2 *P. hermannsburgensis* n=8, *N. alexis* n=6. In trial 3 *P. hermannsburgensis* n=7, *N. alexis* n=6. **P*<0.05; ***P*<0.01; ****P*<0.001. Full names of plant species are given in Table 6.1.





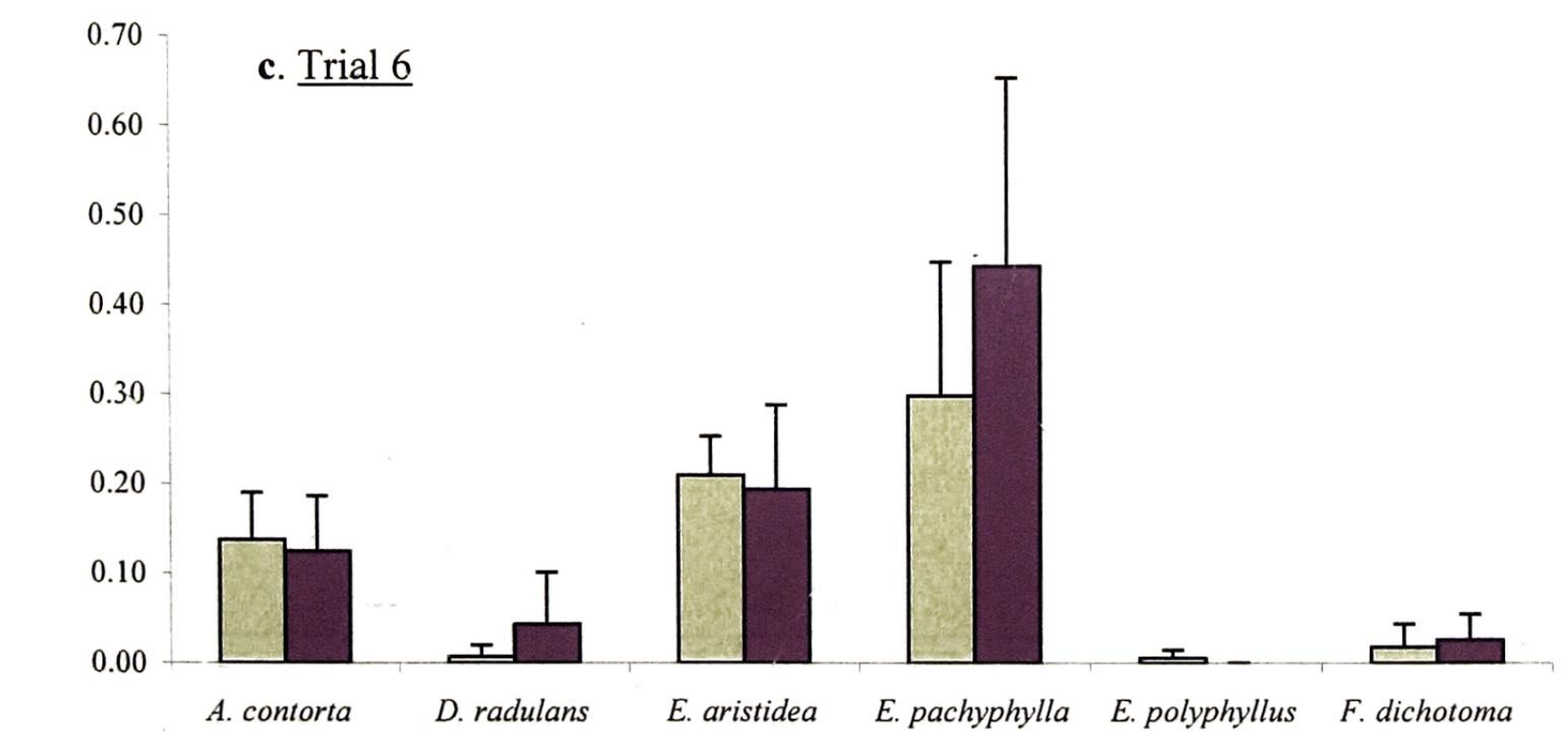


Figure 6.2 **a**, **b**, **c**. Average seed consumption corrected by BMR (Basal Metabolic Rate) + SD of the two rodent species in trial 4 (**a**), 5 (**b**), and 6 (**c**). *P. hermannsburgensis* n=7, *N. alexis* n=6. *$P<0.05$. Full names of plant species are given in Table 6.1.

trial 3 (Figure 6.1**c**). In trial 4 (Figure 6.2**a**) *Trianthema pilosa* was consumed significantly more by *P. hermannsburgensis* than *N. alexis*. In all remaining trials (Figures 6.2**b**, **c**, and 6.3) the two rodent species consumed similar amounts of each native seed species. The total amount of seed eaten changed amongst trials. *Pseudomys hermannsburgensis*, despite being the smaller of the two rodent species, consumed more of certain seed species. In trial 4 it was the major consumer of the species offered. Moreover, *P. hermannsburgensis* seemed to eat a greater amount of Poaceae species (compare Results of Chapter 4), and in general species of smaller dimensions; an exception was *Acacia georginae*, which produces large seeds. *N. alexis* instead appeared to eat a greater variety of seed species from different families and of larger sizes. In trial 7 the species most consumed by both species was *Eriachne aristidea*, followed by *Trichodesma zeylanicum* for *N. alexis* and *Paractaeneum refractum* for *P. hermannsburgensis* (compare Results of Chapter 4). Major consumption was recorded in trial 6 where *Eucalyptus pachyphylla* was highly consumed by both species. It is important to note that *Triodia basedowii* was one of the least consumed seed species by both species. Both in trial 1 and 7, *P. hermannsburgensis* was the major consumer of this latter species.

Table 6.6 presents the results of the Mantel test on the agreement in selection between the two species in each trial. In trial 2 the two species did not show agreement in seed selection, whilst in all the other trials the two species showed no dissimilarity in their selection of different seed species.

Table 6.6. Results of Mantel's test on the preference of the two rodent species for different seed species in seven trials. Indicated are ***g***, critical level for the test, ***Z***, Mantel's test statistic, ***r***, correlation coefficient, and ***P*** values for the test. The critical values for the whole tests are: 1.645 for $P= 0.050$, 1.960 for $P= 0.025$, and 2.326 for $P=0.010$.

Trials	*g*	*Z*	*r*	*P*
Trial 1	2.1334	0.7912	0.9531	<0.025
Trial 2	1.5789	0.6628	0.4017	>0.050
Trial 3	2.7815	1.5422	0.8947	<0.010
Trial 4	2.299	0.2452	0.7653	<0.025
Trial 5	2.666	3.251	0.8705	<0.010
Trial 6	3.2553	6.8538	0.8963	<0.010
Trial 7	2.4882	10.7268	0.4267	<0.010

Tables 6.7 to 6.10 show the mean consumption of each seed species in the seven trials for both rodent species. From these results it is clear that some species were avoided strongly by both rodents (compare also Tables 4.2 to 4.7 of Chapter 4). It is worth noting

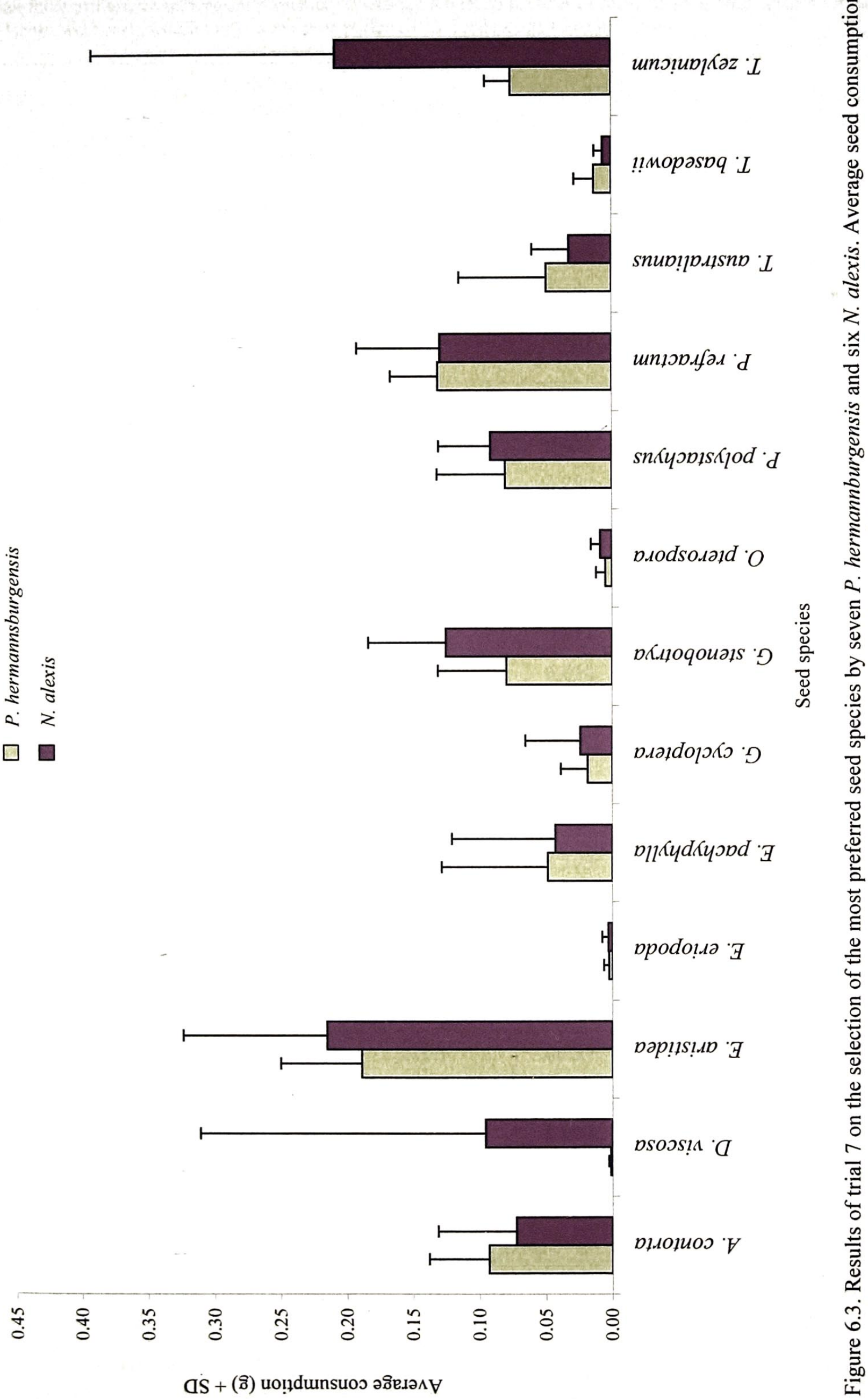


Figure 6.3. Results of trial 7 on the selection of the most preferred seed species by seven *P. hermannburgensis* and six *N. alexis*. Average seed consumption corrected by BMR (Basal Metabolic Rate) + SD. Full names of plant species are given in Table 6.1.

Table 6.7. Selection by *N. alexis* (n=6) of thirty native seed species tested in six trials. Mean consumption and another three preference indices are presented. Ranks are the mean preference ranks of each seed species for each trial. Ranks were assigned giving 1 to the most preferred seed species and n to the least.

Species	Mean consumption (g) ± SD	Manly's a	Vanderploeg and Scavia index	Electivity coefficient	Mean rank
Trial 1					
Cassia artemisioides	0.009 ± 0.009	0.034	0.036	-0.721	4.167
Dicrastylis costelloi	0.021 ± 0.018	0.094	0.097	-0.492	3.667
Grevillea stenobotrya	0.187 ± 0.074	0.664	0.649	0.517	1.000
Trachymene glaucifolia	0.024 ± 0.024	0.072	0.076	-0.509	3.333
Triodia basedowii	0.044 ± 0.035	0.136	0.142	-0.264	2.833
Trial 2					
Cassia pleurocarpa	0.006 ± 0.004	0.017	0.018	-0.866	3.833
Cleome viscosa	0.011 ± 0.006	0.027	0.030	-0.788	3.167
Goodenia cycloptera	0.146 ± 0.068	0.377	0.382	0.187	1.833
Ptilotus polystachyus	0.204 ± 0.009	0.579	0.570	0.382	1.167
Trial 3					
Crotalaria cunninghamii	0.000 ± 0.000	0.000	0.000	-0.996	5.000
Dodonaea viscosa	0.099 ± 0.046	0.210	0.221	0.030	2.333
Eremophila macdonnellii	0.008 ± 0.006	0.019	0.020	-0.821	4.000
Oldenlandia pterospora	0.180 ± 0.169	0.330	0.318	0.013	2.000
Paractaeneum refractum	0.157 ± 0.060	0.441	0.440	0.283	1.667
Trial 4					
Acacia georginae	0.041 ± 0.024	0.422	0.422	0.295	1.667
Newcastelia spodiotricha	0.011 ± 0.011	0.101	0.103	-0.408	3.000
Othonna gregorii	0.015 ± 0.030	0.094	0.094	-0.613	3.500
Stylobasium spathulatum	0.000 ± 0.000	0.000	0.000	-1.000	4.500
Trianthema pilosa	0.043 ± 0.025	0.381	0.380	0.231	1.833
Trial 5					
Acacia dictyophleba	0.054 ± 0.059	0.090	0.099	-0.415	3.000
Eragrostis eriopoda	0.000 ± 0.000	0.000	0.000	-1.000	4.333
Sclerolaena bicornis	0.001 ± 0.002	0.003	0.003	-0.970	3.667
Tragus australianus	0.147 ± 0.095	0.274	0.284	0.025	2.000
Trichodesma zeylanicum	0.279 ± 0.148	0.634	0.614	0.469	1.167
Trial 6					
Aristida contorta	0.125 ± 0.062	0.131	0.150	-0.059	2.833
Dactyloctenium radulans	0.044 ± 0.058	0.031	0.039	-0.688	4.167
Enneapogon polyphyllus	0.000 ± 0.000	0.000	0.000	-1.000	5.167
Eriachne aristidea	0.194 ± 0.095	0.205	0.223	0.049	2.167
Eucalyptus pachyphylla	0.442 ± 0.209	0.610	0.560	0.528	1.000
Fimbristylis dichotoma	0.026 ± 0.029	0.023	0.027	-0.756	4.500

Table 6.8. Thirteen most preferred native seed species tested in the final trial (Trial 7). Mean consumption and another three preference indices are presented for *N. alexis* (n=6). Ranks are the mean preference ranks of each seed species for each trial. Ranks were assigned giving 1 to the most preferred seed species and n to the least.

Species	Mean consumption (g) ± SD	Manly's a	Vanderploeg and Scavia index	Electivity coefficient	Mean rank
Aristida contorta	0.072 ± 0.063	0.050	0.056	-0.281	6.167
Dodonaea viscosa	0.095 ± 0.232	0.083	0.070	-0.708	8.667
Eragrostis eriopoda	0.003 ± 0.005	0.001	0.001	-0.970	10.167
Eriachne aristidea	0.215 ± 0.100	0.225	0.221	0.447	1.833
Eucalyptus pachyphylla	0.043 ± 0.084	0.029	0.030	-0.584	7.667
Goodenia cycloptera	0.024 ± 0.045	0.026	0.028	-0.721	8.500
Grevillea stenobotrya	0.124 ± 0.056	0.134	0.138	0.222	3.667
Oldenlandia pterospora	0.009 ± 0.008	0.013	0.014	-0.745	8.833
Paractaeneum refractum	0.129 ± 0.057	0.122	0.127	0.210	3.833
Ptilotus polystachyus	0.091 ± 0.039	0.088	0.094	0.072	5.167
Tragus australianus	0.032 ± 0.027	0.030	0.033	-0.481	7.833
Trichodesma zeylanicum	0.208 ± 0.186	0.196	0.186	0.241	3.833
Triodia basedowii	0.006 ± 0.006	0.003	0.003	-0.939	10.167

Table 6.9. Selection by *P. hermannsburgensis* (Trial 1 n=9, Trial 2 n=8, Trial 3 to 6 n=7) of thirty native seed species tested in six trials. Mean consumption and other three preference indices are presented. Ranks are the mean preference ranks of each seed species for each trial. Ranks were assigned giving 1 to the most preferred seed species and n to the least.

Species	Mean consumption (g) ± SD	Manly's a	Vanderploeg and Scavia index	Electivity coefficient	Mean rank
Trial 1					
Cassia artemisioides	0.018 ± 0.022	0.071	0.073	-0.530	4.000
Dicrastylis costelloi	0.017 ± 0.010	0.075	0.077	-0.469	3.778
Grevillea stenobotrya	0.098 ± 0.028	0.491	0.484	0.394	1.222
Trachymene glaucifolia	0.024 ± 0.030	0.095	0.096	-0.476	3.889
Triodia basedowii	0.053 ± 0.016	0.268	0.270	0.115	2.111
Trial 2					
Cassia pleurocarpa	0.003 ± 0.003	0.025	0.026	-0.821	3.500
Cleome viscosa	0.025 ± 0.027	0.228	0.228	-0.305	2.250
Goodenia cycloptera	0.016 ± 0.020	0.091	0.093	-0.546	2.875
Ptilotus polystachyus	0.093 ± 0.059	0.657	0.652	0.391	1.250
Trial 3					
Crotalaria cunninghamii	0.000 ± 0.001	0.001	0.001	-0.990	5.000
Dodonaea viscosa	0.082 ± 0.058	0.294	0.295	0.117	2.143
Eremophila macdonnellii	0.005 ± 0.004	0.019	0.020	-0.828	4.000
Oldenlandia pterospora	0.094 ± 0.100	0.271	0.268	-0.003	2.143
Paractaeneum refractum	0.097 ± 0.022	0.415	0.416	0.311	1.714
Trial 4					
Acacia georginae	0.072 ± 0.044	0.352	0.351	0.250	1.571
Newcastelia spodiotricha	0.028 ± 0.028	0.123	0.125	-0.298	3.286
Othonna gregorii	0.021 ± 0.032	0.074	0.075	-0.601	3.857
Stylobasium spathulatum	0.000 ± 0.000	0.000	0.000	-1.000	4.857
Trianthema pilosa	0.078 ± 0.014	0.451	0.449	0.346	1.429
Trial 5					
Acacia dictyophleba	0.026 ± 0.045	0.049	0.053	-0.696	3.714
Eragrostis eriopoda	0.003 ± 0.003	0.005	0.006	-0.946	3.857
Sclerolaena bicornis	0.001 ± 0.001	0.002	0.002	-0.979	4.286
Tragus australianus	0.211 ± 0.050	0.465	0.494	0.395	1.571
Trichodesma zeylanicum	0.226 ± 0.097	0.479	0.494	0.398	1.429
Trial 6					
Aristida contorta	0.150 ± 0.057	0.203	0.257	0.097	2.857
Dactyloctenium radulans	0.008 ± 0.014	0.013	0.017	-0.875	4.786
Enneapogon polyphyllus	0.006 ± 0.010	0.010	0.013	-0.900	4.929
Eriachne aristidea	0.229 ± 0.048	0.318	0.399	0.307	1.714
Eucalyptus pachyphylla	0.325 ± 0.162	0.437	0.516	0.392	1.429
Fimbristylis dichotoma	0.020 ± 0.028	0.020	0.029	-0.786	4.643

Table 6.10. Thirteen most preferred native seed species tested in the final trial (Trial 7). Mean consumption and another three preference indices are presented for *P. hermannsburgensis* (n=7). Ranks are the mean preference ranks of each seed species for each trial. Ranks were assigned giving 1 to the most preferred seed species and n to the least.

Species	Mean consumption (g) ± SD	Manly's a	Vanderploeg and Scavia index	Electivity coefficient	Mean rank
Aristida contorta	0.101 ± 0.049	0.115	0.117	0.189	4.286
Dodonaea viscosa	0.001 ± 0.002	0.001	0.001	-0.969	11.857
Eragrostis eriopoda	0.003 ± 0.004	0.003	0.003	-0.925	11.286
Eriachne aristidea	0.205 ± 0.067	0.261	0.251	0.520	1.429
Eucalyptus pachyphylla	0.053 ± 0.087	0.043	0.043	-0.516	8.000
Goodenia cycloptera	0.020 ± 0.022	0.018	0.019	-0.651	8.857
Grevillea stenobotrya	0.086 ± 0.056	0.107	0.108	0.087	5.143
Oldenlandia pterospora	0.005 ± 0.007	0.005	0.006	-0.873	10.857
Paractaeneum refractum	0.142 ± 0.039	0.182	0.181	0.375	2.714
Ptilotus polystachyus	0.087 ± 0.056	0.090	0.092	0.013	5.286
Tragus australianus	0.053 ± 0.071	0.049	0.050	-0.367	6.714
Trichodesma zeylanicum	0.082 ± 0.021	0.112	0.114	0.125	4.714
Triodia basedowii	0.014 ± 0.016	0.014	0.015	-0.707	9.000

the large variation in selection for *Dodonaea viscosa* and *Trichodesma zeylanicum* in trial 7 for *N. alexis*. This was due to strongly differential consumption by different individuals.

Table 6.11 reports the total seed consumption of each individual across the seven trials.

Table 6.11. Total consumption of seed (g) by each individual of the two rodent species in each trial. *P. hermannsburgensis* (n=9) in trial 1, *P. hermannsburgensis* (n=8) in trial 2, *P. hermannsburgensis* (n=7) trials 3 to 7. *N. alexis* (n=6). M males, F females. The values have been standardised by BMR (basal metabolic rate) of the two species. *** $P<0.001$.

P. hermannsburgensis	**Trial 1**	**Trial 2**	**Trial 3**	**Trial 4**	**Trial 5**	**Trial 6**	**Trial 7**
M 1	0.155	0.144	0.402	0.156	0.459	0.757	0.597
M 2	0.272	0.140	0.337	0.217	0.333	0.765	0.990
M 3	0.200	0.177	0.432	0.150	0.570	1.032	1.333
M 4	0.335	0.231	0.354	0.399	0.522	0.974	1.236
M 5	0.226	0.067	0.098	0.098	0.399	0.506	0.810
F 1	0.186	0.043	0.137	0.144	0.530	0.385	0.471
F 2	0.158	0.175	0.192	0.220	0.454	0.749	0.548
F 3	0.145	0.115					
F 4	0.218						
Average	**0.211**	**0.137**	**0.279**	**0.198**	**0.467**	**0.738**	**0.855**
SD	0.062	0.061	0.134	0.099	0.082	0.232	0.342
N. alexis	**Trial 1**	**Trial 2**	**Trial 3**	**Trial 4**	**Trial 5**	**Trial 6**	**Trial 7**
M 1	0.261	0.305	0.366	0.115	0.288	0.598	0.374
M 2	0.353	0.400	0.621	0.172	0.768	1.312	1.728
M 3	0.245	0.393	0.583	0.036	0.362	0.661	0.763
F 1	0.422	0.469	0.587	0.077	0.469	1.094	1.357
F 2	0.289	0.324	0.117	0.078	0.182	0.244	0.690
F 3	0.145	0.313	0.395	0.178	0.822	1.082	1.401
Average	**0.286**	**0.367**	**0.445**	**0.109**	**0.482**	**0.832**	**1.052**
SD	0.095	0.064	0.193	0.057	0.261	0.398	0.519

***

Large variability in consumption occurred amongst individuals of the same species. *Notomys alexis* ate more seed than *P. hermannsburgensis* only in trial 2. In general, with the increase in number of seed species, there was an increase in the quantity of seed eaten. No significant difference was observed between sexes of either species ($F_{1,5}$=4.54 to $F_{1,5}$=0.06, P>0.05 for *P. hermannsburgensis*, and $F_{1,4}$=0.99 to $F_{1,4}$=0.00, P>0.05 for *N. alexis*). If the initial amount of seed offered is taken into account (Figure 6.4) it is clear that the two rodent species consumed only a fraction of the available seed.

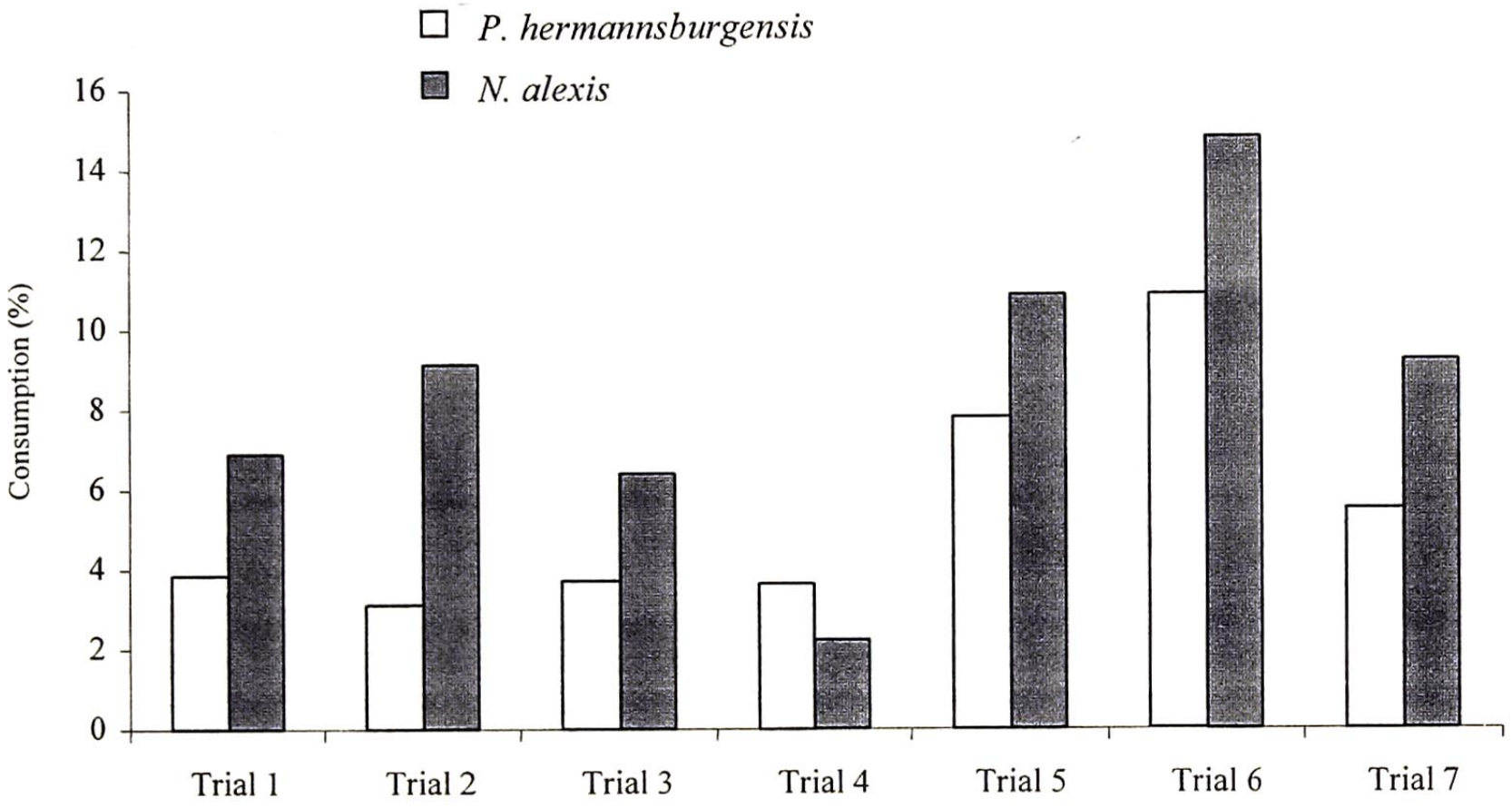


Figure 6.4. Percentage of the total seed consumed of the total amount of seed offered to the two species in seven trials.

However, it is important to remember that husks and diaspores that mice discarded while foraging represent a good part of the initial mass of seed presented (see Table 14 – Appendix 16). The highest percentages of consumption were recorded in trials 5 and 6 for both species. In the comparison of the difference in mean total consumption amongst trials, it appeared that there was considerable variability in consumption between trials (P<0.05), with only few exceptions. However, when the probability values were readjusted using sequential Bonferroni correction, the significance was usually lost (Table 6.12).

Table 6.12. *P* values for the comparison of the difference in total mean consumption of seed amongst trials for *P. hermannsburgensis* and *N. alexis*. The Wilcoxon signed ranks test was used in the analysis. Note that bold represents *P* values <0.05, and that **α** represents the corrected probability value using sequential Bonferroni procedure.

P. hermann.	**Trial 1**	**α**	**Trial 2**	**α**	**Trial 3**	**α**	**Trial 4**	**α**	**Trial 5**	**α**	**Trial 6**
Trial 2	**0.025**	0.010									
Trial 3	0.310		**0.018**	0.010							
Trial 4	0.735		**0.043**	0.013	0.398						
Trial 5	**0.018**	0.008	**0.018**	0.010	**0.028**	0.017	**0.018**	0.017			
Trial 6	**0.018**	0.008	**0.018**	0.010	**0.018**	0.013	**0.018**	0.017	**0.043**	**0.05**	
Trial 7	**0.018**	0.008	**0.018**	0.010	**0.018**	0.013	**0.018**	0.017	**0.028**	0.025	0.128
N. alexis	**Trial 1**	**α**	**Trial 2**	**α**	**Trial 3**	**α**	**Trial 4**	**α**	**Trial 5**	**α**	**Trial 6**
Trial 2	**0.028**	0.008									
Trial 3	0.116		0.249								
Trial 4	**0.046**	0.010	**0.028**	0.010	**0.028**	0.013					
Trial 5	0.116		0.753		0.917		**0.028**	0.017			
Trial 6	**0.046**	0.010	**0.046**	0.013	**0.028**	0.013	**0.028**	0.017	**0.028**	0.025	
Trial 7	**0.028**	0.008	**0.028**	0.010	**0.028**	0.013	**0.028**	0.017	**0.028**	0.025	0.075

In further comparisons among trials, the two rodent species appeared to consume more seed when the choice was limited to few seed species (Figure 6.5 and 6.6). *Eucaliptus pachyphylla*, *Oldenlandia pterospora* and *Tragus australianus* are good examples. In some cases, the difference in consumption was quite large; in others, the difference was minimal, suggesting that those species are the ones actively selected for or avoided, no matter how many other seed species were presented. For both rodent species, three seeds were consumed equally and independently of the number of seed species presented: *Eriachne aristidea*, *Grevillea stenobotrya* and *Eragrostis eriopoda*. Other seed species were consumed variably by the two species.

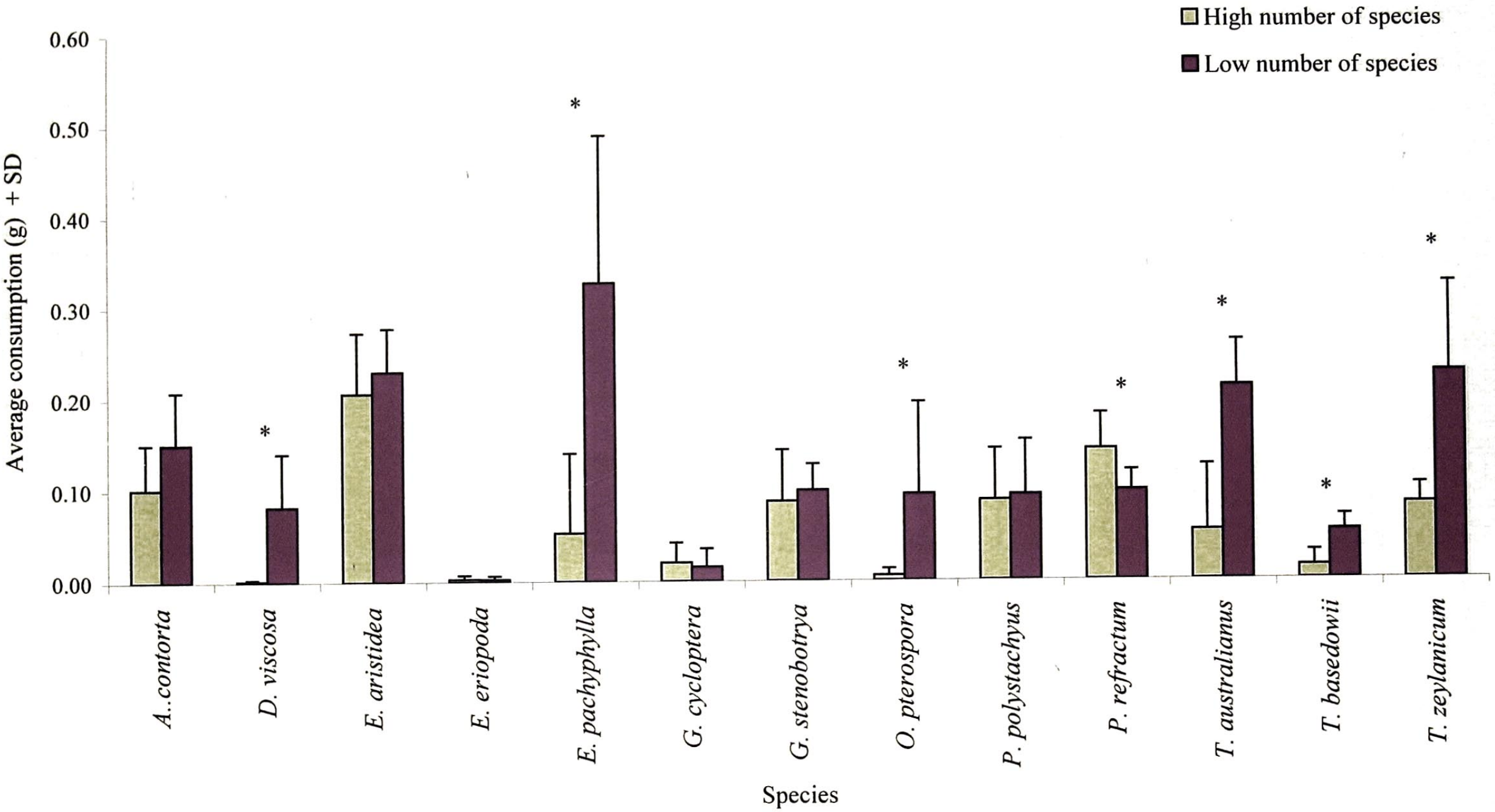


Figure 6.5. Comparison of the consumption of native seed species by *P. hermannsburgensis* (trial 1 n=9, trial 2 n=8, trial 3-7 n=7) between trial 7, which presented a high number of seed species, and trials 1 to 6 which had low numbers of species. The Wilcoxon signed ranks test was applied to obtain *P* values. *$P<0.05$. Full names of plant species are given in Table 6.1.

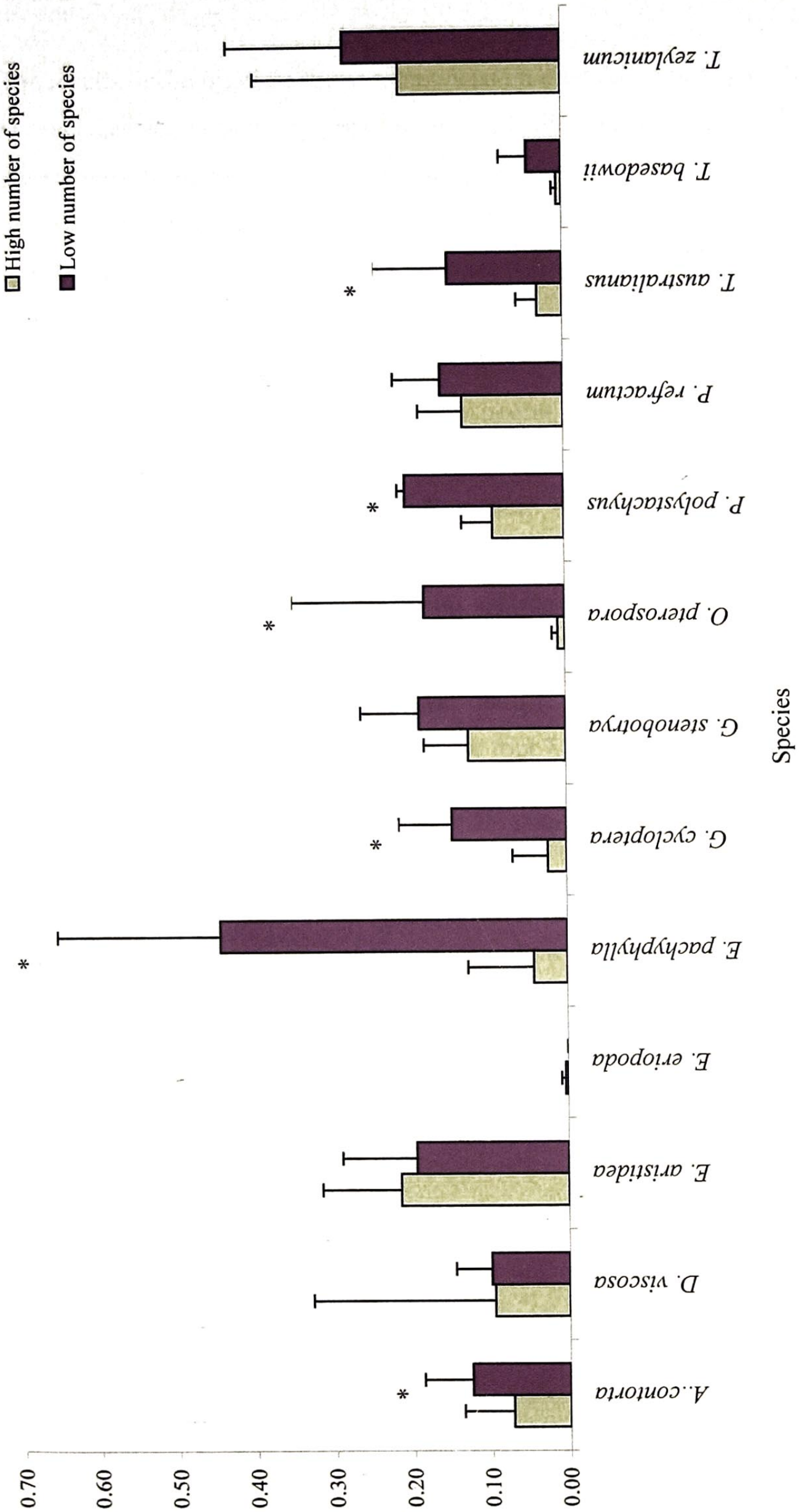


Figure 6.6. Comparison of the consumption of native seed species by *N. alexis* (n=6) between trial 7, which had a high number of seed species, and trials 1 to 6 which had low numbers of species. The Wilcoxon signed ranks test was applied to obtain *P* values. *$P<0.05$. Full names of plant species are given in Table 6.1.

6.3.4. Regression analyses

The results of the multiple linear regressions on seed consumption in the first six trials for both species produced a large number of significant models with extremely high R^2 and F values. Because of the low numbers of observations the results of these tests are not likely to be reliable and are not presented in this chapter (see Appendix 17-20, Tables 15-18). Highly correlated variables were first identified and only one at a time of these correlated variables was chosen for entry into the regression model to avoid collinearity, and the best fit of all was chosen. Water content and Energy content were often negatively correlated, and so were water content and dry matter, because of the methodology chosen to calculate these latter characteristics. Mass and LLD (largest linear dimension) and *N. alexis* and *P. hermannsburgensis* handling time results were also often correlated. However, the variables that produced the best fits according to the Akaike Information Criterion (AIC) in these trials were: +Carbon, -Hardness, (+ or -) Water, -Nht, +Ash, (+ or -) Protein, -Energy, -LLD, -Mass, and -Dry Matter for *P. hermannsburgensis*, and +Hydrogen, -Mass, (+ or -) Hardness, +Ash, -Energy, -Water for *N. alexis*.

Tables 6.13 and 6.14 present the models for trial 7 for the two species of rodents.

Table 6.13. Models of multiple regression on characteristics of seeds consumed by *P. hermannsburgensis* in trial 7. The model with the lowest AIC is in bold and represents the best fit. R^2 and P values for each model are presented in separate columns. AIC (Akaike Information Criterion) is used to compare different models. See text for explanation of variables used in models.

Exp #	Model	R^2	AIC	P
7	**Water-Protein-LLD-LLDE/H-Nht**	**0.807**	**20.897**	**0.019**
7	LLD-Nht-Ash	0.671	23.835	0.015
7	LLD-Nht	0.608	24.138	0.009
7	Energy-Protein-LLD-wE/H-Nht	0.748	24.388	0.045
7	Water-LLD-LLDE/H-Nht	0.697	24.783	0.032
7	LLD-LLDE/H-Nht-Energy	0.683	25.346	0.038
7	Protein-LLD-Nht	0.620	25.728	0.028
7	Mass-LLD-Nht	0.613	25.958	0.030
7	Energy-LLD-Nht	0.613	25.964	0.030
7	Protein-Mass-LLD-Nht	0.667	25.986	0.045
7	Pht-LLD-Nht	0.611	26.029	0.031
7	Water-LLD-Nht	0.608	26.124	0.031

Table 6.14. Models of multiple regression on characteristics of seeds consumed by *N. alexis* in trial 7. The model with the lowest AIC is in bold and represents the best fit. R^2 and P values for each model are presented in separate columns. AIC (Akaike Information Criterion) is used to compare different models. See text for explanation of variables used in models.

Exp #	Model	R^2	AIC	P
7	**Water-Protein-LLD-LLDE/H-*N*ht**	**0.809**	**15.595**	**0.019**
7	Water-Protein-LLD-LLDE/H-Mass-*N*ht	0.824	16.533	0.041
7	Ash-Water-Protein-LLD-LLDE/H-*N*ht	0.822	16.708	0.043
7	Energy-Protein-LLD-mE/H-*N*ht	0.768	18.123	0.035
7	Protein-Mass-LLD-*N*ht	0.694	19.742	0.033
7	LLD-LLDE/H-*N*ht-Energy	0.681	20.264	0.038
7	Water-LLD-LLDE/H-*N*ht	0.658	21.194	0.050
7	Water-LLD-*N*ht	0.594	21.400	0.036
7	Mass-LLD-*N*ht	0.593	21.437	0.037
7	*P*ht-LLD-*N*ht	0.573	22.058	0.045
7	LLD-*N*ht	0.502	22.062	0.031
7	Energy-LLD-*N*ht	0.566	22.267	0.048
7	LLD	0.404	22.411	0.020

In both cases the best fit according to AIC was the same: Water, Protein, LLD, LLDE/H, and *N*ht were the variables that best explained the selection of seeds in the two rodent species (Tables 6.15 and 6.16).

Table 6.15. The best model for trial 7 for *P. hermannsburgensis*. R^2, F, degrees of freedom and P values are reported below the model. Rank = mean preference rank for dietary items.

P. hermann.	Rank = - 24.592 + 61.177 **Water** + 26.603 **Protein** - 11.510 **LLD** + 5.119 **LLDE/H** + 6.964 ***N*ht** R^2=0.807 $F_{5,7}$=5.863 P=0.019

Table 6.16. The best model for trial 7 is presented for *N. alexis*. R^2, F, degrees of freedom and P values are reported below the model. Rank = mean preference rank for dietary items.

N. alexis	Rank = - 26.581 + 73.558 **Water** + 25.548 **Protein** - 9.905 **LLD** + 4.061 **LLDE/H** + 5.761 ***N*ht** R^2=0.809 $F_{5,7}$=5.936 P=0.019

The two models are very similar. The mice appeared to select seeds for high water content and protein, and for seed species with a relatively larger embryo compared to the total size of the seed. Conversely, they selected against seed species with large dimensions,

even if the positive *N. alexis* handling time could suggest choice of larger species. The presence of *N. alexis* handling time in both models can be explained considering that *P. hermannsburgensis* handling time is highly correlated with and very similar to that of *N. alexis*. It seems also that because *N. alexis* handling time is positive, the rodents chose seeds that were more difficult to handle or husk, and were not constrained by the time spent in foraging.

6.4. Discussion

The results of this chapter indicate that captive *P. hermannsburgensis* and *N. alexis* selected some native seed species over others on the basis of their protein, water content, kernel size relative to the entire seed, and small dimensions. Moreover, they did not seem to be constrained by the time necessary to handle and process the seeds.

Within the two species the concordance in choice was usually high, depending on the number and the type of seed species presented. The limited variability that did occur amongst individuals of the same species was perhaps due to the absence of any particularly palatable seed species in some trials, or seeds rich in the characteristics that mice select for. In this case each individual would have faced limitations with respect to seed choice, compromising in various ways amongst the characteristics offered. Familiarity also can play an important role in individual food choice (Mares and Williams 1977, Gillingham and Bunnell 1989).

In trial 7 *N. alexis* individuals did not show their strongest agreement in seed selection, but they did show the highest seed consumption of all the trials. *Pseudomys hermannsburgensis* also consumed more seeds in the last two trials, in which the number of seed species and therefore potential for variability was highest. These findings contradict the results of Murray and Dickman (1997) who observed a five-fold decrease in overall consumption between a trial with six native seed species and a trial with ten species. Differences in food consumption between trials and species are often very noticeable within rodents. In the present trials, however, *N. alexis* consumed significantly more than *P. hermannsburgensis* only once during the seven trials, even though the larger species tended to consume absolutely more each night on all occasions except trial 4. Because of its smaller mass, the basal metabolic rate of *P. hermannsburgensis* is higher and so therefore is its daily energy budget scaled for mass (Predavec 1997b, McNab 1988). It is likely that *P. hermannsburgensis* has to spend longer in foraging to fulfil its energetic needs, and it may be that it is less selective than *N. alexis*. However, *P. hermannsburgensis*

still took a broad range of seeds and it would seem that energetic constraints were not a limiting factor in this study.

When the percentage consumption of seeds is considered, it is clear that average intake of each seed species should decrease when the number of seed species increases. This could be due to longer times spent in sampling the range of seeds, and in decision taking, since 'partial sampling' is always important in choosing seeds (Murray and Dickman 1997). Another explanation could be that once animals have fulfilled their nutritional and energetic needs, they stop foraging or decrease their food intake, spending time in alternative activities, thus maximising their energetic benefit from foraging. Continuing foraging when food density has decreased and when the basic needs are fulfilled would be risky and energetically expensive, especially in nature where other external factors play important roles (Brown *et al*. 1994a, b, 1997). Brown (1988) quantified the extent to which a rodent uses a seed resource patch under predation risk by measuring the density of seeds remaining in a resource patch abandoned by the forager. This density, called giving-up density (GUD), is a measure of foraging efficiency defined as a ratio of output to input; that is, the harvest rate of resources divided by the sum of energetic foraging costs, predation costs and missed opportunity costs (Brown 1988, but see also Price and Correll 2001). Kotler *et al*. (1994) reviewed the role of predation in shaping the foraging behaviour, morphology and community organization of desert rodents, and concluded that its effects are pervasive. It would be interesting refine the experiments of this chapter in the field using GUD trays to compare how the selection changes under predation risk.

The fact that the two species showed identical selection coefficients based on few seed characteristics and that their concordance in preference was quite high, means that both species are likely limited by the same constraints. The way they face these limitations can be slightly different, and dependent on their morphological, behavioural and physiological characteristics. Differences in metabolism, digestive capability, size and microhabitat use, are examples of these species-specific traits. Such differences could explain the differential selection of native seed species observed in some trials. For example, the bipedal morphology of *N. alexis* may render it faster than *P. hermannsburgensis* in acquiring and processing seeds. This means that the latter species has to spend more time to obtain the same amount of food, and thus would show a corresponding increase in energy spent. *Pseudomys hermannsburgensis* may not maximise its rate of energy intake while foraging, at least by decreasing its handling time, but may select seeds that are quicker to process. In the results it appeared that *P. hermannsburgensis* did in some cases select for and consume

more smaller species in comparison with *N. alexis* (e.g. *Tragus australianus*, *Triodia basedowii*, *Cleome viscosa*, *Trianthema pilosa*). Nevertheless, handling time appeared to be positively correlated with seed consumption, perhaps meaning that the rodents were first satisfying nutritional rather than energetic needs; similar conclusions were reached also by Reichman (1977).

The results of this research also suggest that food choice results from a compromise amongst several characteristics of food, both nutritional and morphological, as similarly found by Karasov (1985) and Henderson (1990). Often, studies in the literature have focused on only a single characteristic, and have found this to be responsible for food preference in rodents. In their natural environment it is highly probable that rodents optimise their diet by choosing to ingest the most appropriate seeds as determined by a vast range of trade offs such as availability, search time, handling time, predation risk, nutrient content, moisture, and the secondary defence mechanisms of the seeds.

The selection for high seed water content is in agreement with the results of Chapter 5, and with Frank (1988a, b). Desert rodents extract most of the water they need from their food, either as free or metabolic water. The ability to detect and select for free water content in seeds would be of great advantage in periods of drought. The results of this chapter again contradict the predictions of Model 1 in Chapter 4, that rodents are limited by free water in their environment. Moreover, during dry periods, rodents are likely to feed on carbohydrate-rich foods, due to the scarcity of fresh green plant material, and seeds. Carbohydrates yield the most water per unit of metabolic energy (Hulbert and MacMillen 1988), so granting the animals their water requirement in the absence of free water. When rodents select for free water in their food (as also shown in Chapter 5), at the same time they free themselves from the constraint of maximising their intake of metabolic water from the food. This enables them to fully exploit the protein content of food that gives the least water per unit of metabolic energy (Hulbert and MacMillen 1988). Consequently, free water and protein content should be present together as characteristics selected for in seeds.

The selection for protein content found in this study reflects the results of previous research (Tenore 1977, Henderson 1990, White 1993, 2002, Gutiérrez and Bozinovic 1998). It is thought that animals are often more likely to be limited by nitrogen than energy in their food, especially in environments as poor in nutrients such as deserts (White 1993, 2002). The two species always husked the seeds offered, so maximising the protein to fibre ratio (Milton 1979, Gutiérrez and Bozinovic 1998). Husks are rich in fibres and carbohydrates, but relatively low in proteins. Moreover, Poaceae is one of the families

most strongly represented in the diet (compare Chapter 4) and in the seeds selected by the two species. This family is almost entirely represented in this study by annual or short-lived perennial grasses, with the exception of the long-lived *Triodia basedowii*. Such grasses proliferate after rainfall, initiating their growth and seed production by mobilising nitrogen from the soil into their tissues and seeds. Often, green grasses have been associated with an increase in reproduction in rodents (Chew and Butterworth 1964, Beatley 1969, Batzli and Pitelka 1971, Negus and Berger 1977, White 1993, 2002). The green seeds are likely to contain essential amino acids that can trigger reproduction (Sano and Kawashima 1982, Allen and Hume 1997, Rozan *et al*. 2001). Rodents may profitably identify and utilise these species as the 'good species' for reproduction. In addition, most of these grass species lack toxic secondary compounds that contradistinguish them from species in other families (e.g. Apiaceae, Asteraceae, Boraginaceae, Chenopodiaceae, Euphorbiaceae, Fabaceae) (R. McKenzie *pers. comm*.), hence increasing palatability.

Morphological characteristics of the seeds also appeared to be important in their selection by the rodents. The physical structure of a seed clearly will affect the ability of a mouse to eat it. Factors such as mass, size, hardness, and seed structure (e.g. presence of sharp spines) can greatly modify how a seed is perceived by a forager (Price 1983a). The rodent first has to process the seed in order to absorb its nutrients. Some seed species in my trials were almost or totally untouched (such as *Cassia pleurocarpa*, *Crotalaria cunninghamii*, *Dactylocteneum radulans*, *Eragrostis eriopoda*, *Eremophila macdonnellii*, *Sclerolaena bicornis*, *Stylobasium spathulatum*). Most of these seed species are rich in free water or protein, but were probably selected against on the basis of their seed coat hardness or structure (*Eragrostis eriopoda*, *Eremophila macdonnellii*, *Sclerolaena bicornis*, *Stylobasium spathulatum*), handling time (*Cassia pleurocarpa*), or presence of toxins in the coat or in the seed itself (*Crotalaria cunninghamii*, *Dactylocteneum radulans*).

The influence of seed size on preference has been much studied in the Heteromyidae of North America. It has been suggested that seed size selection is related to the body size of the predator (Smith 1942, Brown and Lieberman 1973, Mares and Williams 1977, Price 1983a), but this has been disputed (Smigel and Rosenzweig 1974, Brown *et al*. 1975). Results of this chapter showed that the two species usually select against seed species with a long linear dimension (but cf. Henderson 1990), both preferring small species to larger species regardless of the rodents' own size. Smaller seed species are quicker to handle and therefore yield a higher net intake of nutrients per unit time. However, the handling time of *N. alexis* was correlated positively with seed consumption in both rodent species. This

presents a contradictory result, and suggests perhaps that small seed species are not always easier and faster to handle. Rodents probably select food items from within a range of sizes, and in doing so will completely eat the seeds inside that size range. They can only partially consume larger seeds (personal observations of the final seed mix of the trials, indicated that bigger seeds were often only partially eaten). In this way, rodents usually ate seeds of similar size. However, it is important to remember that LLD is an indication of just one seed dimension, because seeds with long seed coats can have very small kernels inside, as often happens with grass seeds with long awns and small grains. For this reason it is crucial to distinguish between a single linear dimension and the overall seed shape (McNaught 1994), and between the size of the kernel and the size of the entire seed. The kernel ratio to the size of the entire seed is likely to be more indicative of the quality of the seed as perceived by the forager, because it gives an indication of the reward that the forager gains after the time spent in processing the seed. My results showed that consumption increased with an increase in the relative kernel size of the entire seed.

Intriguingly, handling time for *N. alexis* seemed to better explain the regression results than *P. hermannsburgensis* handling time, even for the latter species. This may imply that *P. hermannsburgensis* should consume seeds at the same speed as *N. alexis*, although it should be noted that handling time for the two species were highly correlated and similar. The positive handling time in the models means that relatively long periods were spent in processing food items, especially large ones. The two species do not seem to be constrained by time when foraging. This can be explained by the lack of external pressures to which the rodents were subjected in captivity. Absence of predation, competition, minimal search time, and vicinity to a clumped food resource, would reduce foraging to a need to satisfy nutritional and energetic demands with little reference to trade-offs imposed by such multiple pressures. These are some of the limitations of my experiment.

Captive animals likely select food items primarily on a nutritional basis, and are quite selective. It is probable that the rodents perceive seeds in laboratory trials as being high in density and availability, and so become more discriminating (Emlen 1966, MacArthur and Pianka 1966, Smigel and Rosenzweig 1974). However, they may still eat seeds that they would have avoided in their natural environment. Smigel and Rosenzweig (1974) predicted that dietary diversity would diminish when seed density was high. This seems not to be the case in this study, where it was not the dietary diversity that diminished when availability and variety of seeds increased (compare seed species eaten in exp 1 to 6 and in exp 7), but rather the percentage of amount of seed eaten of the total offered (Figure 6.4). Thus, when

presented with a high variety of seed types, rodents do not limit their foraging to few species to fulfil their nutritional needs but exploit, to different extents, all the resources available. It is possible that, when presented with a large choice of different seed species and not limited by time, rodents select not only the 'best' species but also the 'best' seeds within each species (e.g. fresher and greener seeds). In this way they cream off the best resources present, and not only satisfy their basic need to survive, but maximise the intake of 'good food' to be able to grow and reproduce. This scenario is likely to happen every time desert life explodes after a series of rainfall events. Green plant material, green seeds, mobilised nitrogen and a large variety of seed species are the probable staples of rodent eruptions in Australian desert environments.

Unlike heteromyid rodents that transport unhusked seeds to their burrows (e.g. Price *et al.* 2000), Australian species do not appear to carry or cache their seeds and must therefore process their seeds on the spot (C. Dickman *pers. obs.*, S. Ricci *pers. obs.*) partially or totally husking them. Consequently, they may be more selective while foraging, because they cannot choose later in the safety of their burrow amongst a variety of seeds collected, but have to extract their nutrient and/or energy requirements immediately (Reichman 1977).

A frequent objection to laboratory trials is that captive rodents are likely not to be limited by nutritional constraints, and so may be less selective (they can afford to eat poor quality food) or more selective (they can afford to pass up poor quality or unpalatable food) than in the field. After 24 hours of starvation, as imposed in my trials, an animal could be expected to be hungry and to react to the presence of food in a similar way to that in its natural environment. Moreover, every time an animal forages, it presumably responds to instincts that have been selected by a long process of evolution, and can be expected always to behave so as to maximise its fitness.

In this chapter I focused my attention on the granivorous part of the broader omnivorous diet of the two study species. However, the two species exhibit quite variable diet over the year (Murray and Dickman 1994a, Chapter 4), consuming invertebrates in greater proportion in autumn. Invertebrates are very rich in proteins and water and can be a good substitute for seeds and plant material when these latter resources are too scarce to fulfil the nutritional needs of the two rodent species. Invertebrates are in fact eaten throughout the year by many omnivorous rodents as a supplement to their diet (White 1993). It was not possible to incorporate choice tests for the two study species in this work, although it would be a profitable direction for research in this area to take in future.

Another point to be noted is the high variability in response exhibited by the same species in different studies. The findings of Murray and Dickman (1994a) and McNaught (1994) on the same rodent species do not always agree with the results of this chapter. For example, the earlier studies found that both study species selected *Triodia basedowii* seed, whereas in this study it was avoided. One explanation is that different techniques and methodologies led to different results. Another explanation is that animals were offered seed species in the different studies that were similar in the balance of several characteristics that make them suitable as food sources, so that individual rodents could have benefited from eating a wide variety of combinations of seeds. Hence, strong patterns of selection for particular species would not be expected. Seeds of the same species also change dramatically in their nutrients and free water over time (Sano and Kawashima 1982, White 1993, Allen and Hume 1997, Rozan *et al*. 2001). This is demonstrated by the differential results of nutritional analyses performed on the same seed species in Murray and Dickman (1994a) and in this study (Appendix 16, Table 14). Thus, rodents may select for similar characteristics of food in different studies, but our interpretation of the results is biased by an incomplete knowledge of what we are offering to them each time.

6.5. Conclusions

In conclusion, *P. hermannsburgensis* and *N. alexis* appeared to select for certain characteristics of seeds in captive selection trials. Protein and free water content were the nutritional characteristics the two species most preferred in the seeds. The seed species were also selected on the basis of their kernel size, the part eaten by the mice. Not much variability in selection was observed between the two species.

These findings are, however, limited by being obtained in an extremely simplified environment without external constraints and pressures. In their natural habitats mice have to search for and find the seeds to be able to satisfy their nutritional and energetic requirements. Differential access to different seeds in the field may be important in restricting the diversity of seeds that rodents are exposed to, and may also be important in differentiating foraging strategies and thus in reducing competition between the two species.

In the next chapter I will investigate seed detection by the two rodent species at different depths in soil and at different dispersions in further laboratory trials.

CHAPTER 7: SEED DETECTION BY RODENTS: EFFECTS OF SEED DEPTH AND DISPERSION

7.1. Introduction

Seeds in deserts are dispersed in a complex pattern of clumped and scattered distributions. Biotic (seed shape and size, dispersal patterns, animal dispersers) and abiotic (wind, water, soil microtopography and structure) factors all influence seed distributions (Reichman 1979, McIntyre 2001). Consequently, different microhabitats have different seed distributions (Nelson and Chew 1977, Reichman and Oberstein 1977, Frye and Rosenzweig 1980, Price and Reichman 1987), with open areas often characterised by clumped seed dispersions and under-shrub areas by scattered seed dispersions. Highly clumped seed dispersions usually occur in open areas because of dispersal into wind-shadows and depressions by wind and rain (Reichman 1979, McIntyre 2001). Seeds principally accumulate in under-shrub areas in scattered dispersions after falling from the parent plant to the surface in the initial phase of dispersal (McIntyre 2001). The vertical distribution of seeds in desert soils depends on seed morphology, soil particle size and structure, soil burial processes and distance from the mother plants (Childs and Goodall 1973, Nelson and Chew 1977, Price and Brown 1983, Reichman 1984, Price and Reichman 1987, Guo *et al.* 1998) with most of the seeds concentrated in the top 2 cm.

Foraging in a patchy environment involves energetic costs and benefits, so that the searching and handling efficiency of a predator will often be important components of its success (Krebs and Kacelnik 1991, McNaught 1994). In the particular case of seed-eating predators, seeds can be inaccessible because they are physically impossible to obtain or because the costs of collecting them exceed the gains. Inaccessibility of seeds to foragers can be due to: 1) unfavourable seed distribution (clumped or scattered pattern), 2) depth in soil, 3) density, and 4) physical inaccessibility (e.g. seeds are high above ground or in inaccessible microhabitats). All these factors greatly affect foraging opportunities and dictate both harvest rates and search costs by granivores (Price 1983a, Price and Heinz 1984).

Numerous studies have documented the effect of seed distribution and depth on the foraging behaviour of the heteromyids of North America. According to 'the clump size selection' hypothesis the use of clumped seeds is associated primarily with the use of open microhabitats by bipedal and larger species, while the use of scattered seeds is coupled with

the use of under-shrub microhabitat by quadrupedal, smaller species (Smigel and Rosenzweig 1974, Mares and Williams 1977, Reichman and Oberstein 1977, Price 1978, Bowers 1982). Seeds can be gathered more quickly if clumped; the harvest rate then increases and the handling time potentially decreases (Pulliam 1974, Price and Heinz 1984, Kotler *et al.* 1993), although search time for clumps is possibly higher (Thompson *et al.* 1980). Bipeds that travel more rapidly than similar-sized quadrupeds (Garland 1983) may be better able to exploit widely spaced clumps in open spaces (Reichman 1981, Price 1983b) as well as being better able to escape predators if seen in the open (Bouskila 1995). Nevertheless, on occasions, heteromyids are opportunistic and exploit clumps regardless of clump size, and their own locomotion and size (Frye and Rosenzweig 1980, Stephens *et al.* 1986). Seed distributions in Australian deserts appear to be similar to those in North American deserts (Kemp 1989). Seeds tend to clump in open areas in a patchy pattern, and to scatter more uniformly under shrubs or in the proximity of parent plants. McNaught (1994) studied the ability of *N. alexis* to recover millet seeds from two different dispersions at two different depths, and demonstrated that this species did not show any particular preference for the two dispersions, exploiting them equally.

Rodents are thought to detect and recover buried seeds by olfaction (Howard and Cole 1967, Lockard and Lockard 1971, Johnson and Jorgensen 1981, Randall 1993, Vander Wall 1993, 1995b, 1998), but they can also use soil disturbances as a sign of seed presence (Reichman 1979), or employ learning skills to remember the location of food patches (Rebar 1995).

The ability to find buried seeds can be very advantageous in a desert environment where the seed supply on the surface is extremely variable, and where the top centimeters of soil, in particular, are rich in seeds (Reichman 1979, Guo *et al.* 1998). Studies on heteromyids in North America show the ability of these rodents to detect seeds at depths of 0.5 - 20 cm, albeit with some physical clues needing to be left for the animals to dig at this latter depth (Reynolds 1958, Howard and Cole 1967, Lockard and Lockard 1971, Perkins *et al.* 1976, Reichman and Oberstein 1977, Vander Wall 1993, 1998). A sharp increase in detectability was observed if the seeds (Vander Wall 1993, 1998) or the sand (Johnson and Jorgensen 1981, Vander Wall 1995b) were hydrated. Seeds are very hygroscopic, rapidly absorbing water from the surrounding environment. This moisture facilitates the release of odorant molecules from the seeds, which rodents can readily detect (Vander Wall 1998). Reichman and Oberstein (1977) found that bipedal and larger heteromyids were better able to use clumped seeds than quadrupedal and smaller heteromyids partly because of the

greater ability of the former to locate buried caches. They hypothesised that this greater detection ability was due to their rapid movements that allowed them to discern sharp contrasts in odour. Johnson and Jorgensen (1981), however, working on the same species, found opposite results. Other factors can be involved in seed detection such as soil type and soil particle size, seed species (aromatic qualities can enhance detection), season, rodent size, age and expertise (Johnson and Jorgensen 1981). Exploratory digging can be an integral part of rodents' search behaviour, especially when the location of food is uncertain (Vander Wall 1991). In comparison to American species, Australian rodents are not good at detecting buried seeds, having been observed mainly to use seeds on the surface. McNaught (1994) found that the ability of *N. alexis* to detect buried seeds decreased with depth, from 2 cm to 3 cm. Moreover, Australian desert rodents have not been observed to cache seeds and so have presumably been subjected to less selection to possess good learning skills and memory in order to recover buried caches. Consequently, they are likely to rely more on olfaction cues in their foraging efforts.

In this chapter I tested the ability of *P. hermannsburgensis* and *N. alexis* to detect seed caches buried at different depths, and in different dispersions (scattered and clumped). I also tested the null hypothesis that all distributions of seeds are equally accessible at different depths, and that there is no difference in detection performance between the two species.

7.2. Materials and Methods

All the animals used in this chapter were maintained as described previously (Chapter 5), and were used also in the experiments of Chapters 5 and 6.

Two laboratory experiments were carried out to test the ability of the two species to detect scattered and clumped seeds at different depths. Six *N. alexis* and nine *P. hermannsburgensis* were used in the experiments. No animal was tested over two consecutive nights and a rest period of at least three nights between trials was guaranteed. In order to minimise odour cues, care was put into changing the glass tanks in which animals were tested so that animals were never tested in the same aquarium with the same sand over consecutive trials. Animals were deprived of food for 24 hours before each trial. Before dusk, and just prior to the usual onset of foraging, animals were moved to the experimental glass tanks (160 cm x 60 cm x 40 cm) filled with sand to a depth of 4 cm. One animal was placed in a tank for each trial. Sunflower seeds were used as the experimental seeds because they were readily available, easy to recover after the

experiment due to their relatively large dimensions, and they were the second most preferred commercial seed by the two species in captive trials (S. Ricci *pers. obs.*, Murray and Dickman 1994b). About four grams of seed was used in each experiment for both species as it slightly exceeds the amount the two species were expected to eat in a night (Calver *et al.* 1990, Murray and Dickman 1994b). The seeds were weighed and counted just before the beginning of the trials and then dispersed in the experimental treatments before the animals were moved into the experimental glass tanks. A control was used to monitor eventual water loss and gain, and comprised four grams of seed placed in a glass tank identical to those used for the rodents. Animals were allowed to forage overnight, and removed in the early morning. The experimental aquaria were then sieved and checked thoroughly to collect the remaining seeds and husks. These seeds were weighed and counted again and the amount eaten was calculated. Corrections for water loss and gain were applied as in Chapter 6. The consumption by each individual was expressed both as number of seeds eaten out of the total number of seeds offered, and as the mass of seeds eaten of the total seed mass offered. The mass consumed by each individual was also divided by the individual number of seeds eaten to gain an indication of the size of seeds eaten in the treatments.

At the end of the experiments six samples of one gram of sunflower seeds from the same supply used in the trials were weighed, put in the oven at 70°C for a week, and then weighed again to measure the free water content of the experimental seed. In addition, nine samples of five grams of sand were collected randomly during the experimental procedure, weighed, then put in the oven for a week, and then weighed again to measure the average moisture content of the substrate.

The general procedure followed in the two experiments is described below.

7.2.1. Scattered seeds

Four grams of sunflower seeds were scattered randomly but evenly in the glass tank at three different depths: 0 cm, 2 cm and 3 cm (one depth per trial). In the case of the 2 cm and 3 cm treatments, seeds were buried under the sand. In both cases, all sand was first removed, then refilled to a depth of 2 cm and 1 cm, respectively, and the seeds scattered on this layer. The remaining sand was then spread evenly over the top of the seeds to the required depth. A cotton bag provided shelter for animals during trials of this first experiment. At the end of each trial, seed consumption was calculated as described above.

7.2.2. Clumped seeds

Four grams of sunflower seeds were divided into four smaller one gram clumps. One gram clumps were chosen because this amount was not enough to satiate an animal and so it would have to search for more than one clump during its foraging bout. The clumps were then dispersed at three different depths (one depth per trial: 0 cm, 2 cm, or 3 cm) in random positions as determined by a random number table. In the case of 2 cm and 3 cm depths I used a similar procedure to the one used for the scattered seed experiment. All sand was removed from the tank and then refilled to a depth of 2 cm and 1 cm, respectively. The four clumps were placed onto the sand in random positions and buried with the remaining sand to the required depth. A cotton bag again provided shelter for the test animal. At the end of the trials, the number of clumps recovered was recorded for each treatment, and seed consumption calculated as before.

7.2.3. Analyses

For each rodent species, a paired *t*-test was used to compare seed consumption between the two distributions at each of the different depths, and between depths in the same distribution. All the consumption data were arcsine-transformed to improve normality. This analysis was chosen because the same individuals were run in all the trials.

Seed consumption in the two distributions of seeds and the three depths of seed burial was compared between species using a one-way ANOVA after necessary transformations. The average consumption of the two species was standardised by BMR (Basal Metabolic Rate) using the same procedure as described in Chapter 6. Differences between sexes within each species were initially analysed using the same procedure, and found to be non-significant ($F_{1,4}$=4.16 to $F_{1,4}$=0.01 for clumped seeds, $F_{1,4}$=1.18 to $F_{1,4}$=0.00 for scattered seeds for *N. alexis*, and $F_{1,7}$=1.42 to $F_{1,7}$=0.22 for clumped seeds, $F_{1,7}$=1.10 to $F_{1,7}$=0.09 for scattered seeds for *P. hermannsburgensis*, P>0.05 in all cases), Thus, results for the sexes are pooled in all analyses below.

Because multiple comparisons were made of the same data (e.g. seeds consumed, 0 cm vs 2 cm, 0 cm vs 3 cm, and 2 cm vs 3 cm), it was appropriate to reduce the probability of committing type-1 errors. Hence, if a probability of <0.05 was found, it was readjusted using sequential Bonferroni correction (Quinn and Keough 2002).

7.3. Results

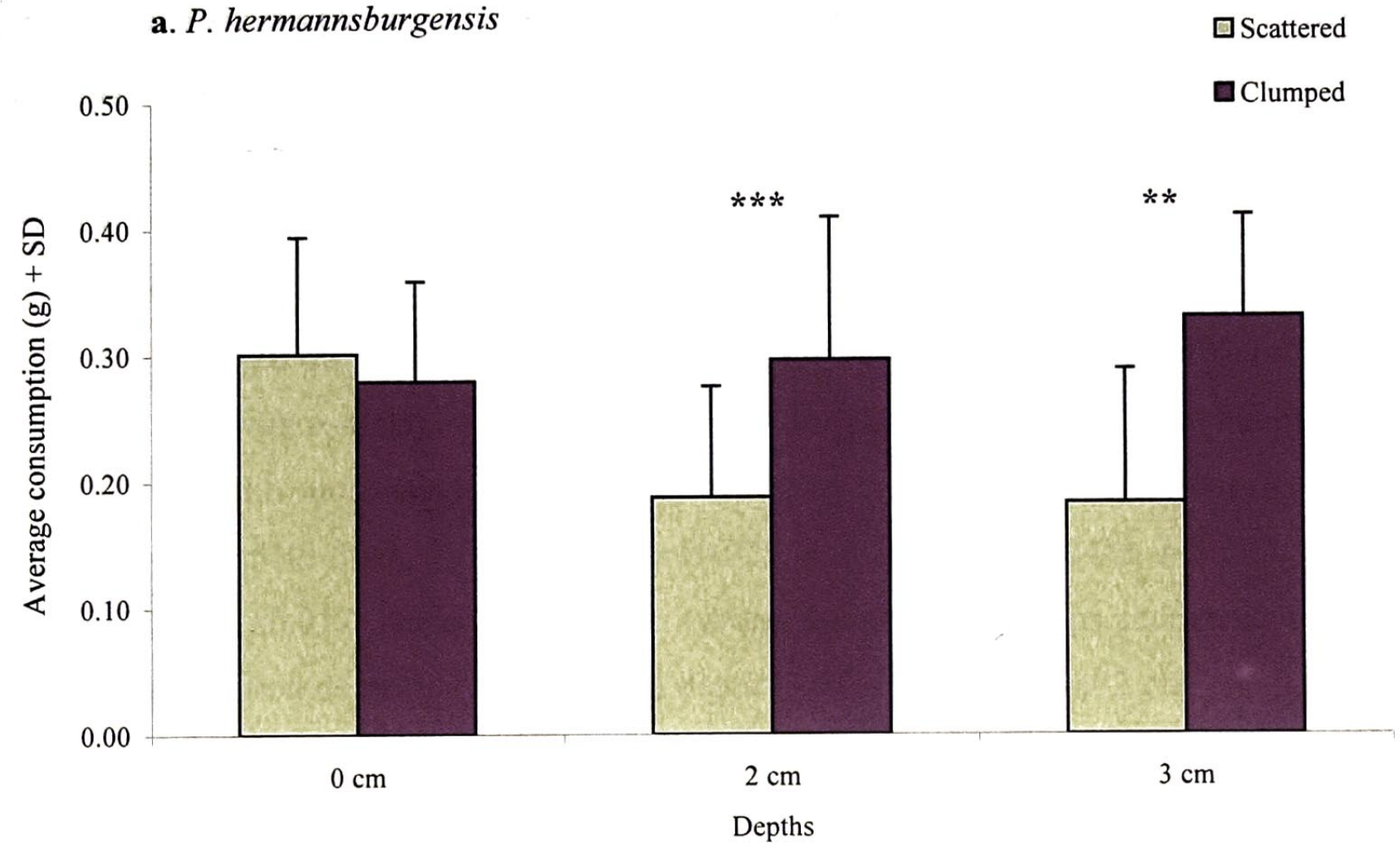
7.3.1 Seed consumption: mass of seeds eaten

In the scattered dispersions, the mean mass of seed consumed by *P. hermannsburgensis* on the surface was much greater than that consumed at 2 cm and 3 cm (30% of available seed consumed on the surface, versus 19% and 18% under the sand, respectively, Figure 7.1**a**). Expressed as grams of seed eaten as a proportion of total grams of seed offered, this species consumed significantly more scattered seeds on the surface than at 2 cm (t=3.384, df=8, P=0.010, with a=0.017). However, there was no difference in consumptions at 0 cm and 3 cm depths and at 2 cm and 3 cm depths in the scattered dispersion (t=2.549, df=8, P=0.034, with a=0.025, and t=0.356, df=8, P>0.05, respectively).

In the clumped distribution, *P. hermannsburgensis* consumed the same amount of seeds at 0 cm and 2 cm (t=-0.374, df=8, P>0.05), while there was a significant difference in the mass of seeds eaten on the surface and at 3 cm (t=-3.744, df=8, P=0.006, with a=0.017). No significant difference was observed between 2 cm and 3 cm depths, even if the consumption was slightly higher at the latter depth (t=-1.629, df=8, P>0.05).

Pseudomys hermannsburgensis was equally successful in foraging for scattered and clumped seeds when the seeds were on the sand surface (t=1.277, df=8, P=0.238, Figure 7.1**a**). For seeds buried 2 cm and 3 cm deep, *P. hermannsburgensis* consumed more seed when clumped than when scattered (30% versus 19%, and 33% versus 18%, respectively, with t=5.254, df=8, P=0.001, with a=0.017, and t=3.483, df=8, P=0.008, with a=0.025, respectively). The mass of seed consumed was similar at 2 cm and 3 cm depths for both dispersions, but in the case of clumped seeds the number of clumps recovered and exploited dropped with depth (averaging 3.67 clumps at 0 cm, 3.22 at 2 cm and 2.78 at 3 cm). This means that rodents exploited more extensively the fewer clumps found at greater depths. Moreover, *P. hermannsburgensis* tended to eat larger seeds at greater depths in both dispersions (scattered seeds: 0.04 ± 0.01 g/seed SD at 0 cm, 0.05 ± 0.02 g/seed SD at 2 cm and 3 cm; clumped seeds: 0.04 ± 0.003 g/seed SD at 0 cm, 0.05 ± 0.004 g/seed SD at 2cm, and 0.05 ± 0.003 g/seed SD at 3 cm).

Notomys alexis showed an equal ability to exploit the three different depths in the scattered dispersion (t=0.754, 0 cm versus 2 cm, t=0.962, 0 cm versus 3 cm, and t=0.138, 2 cm versus 3 cm, df=5, P>0.05 for all, Figure 7.1**b**). In the clumped distribution, *N. alexis* consumed significantly more seeds in the 2 cm and 3 cm depths than on surface (t=-3.473,



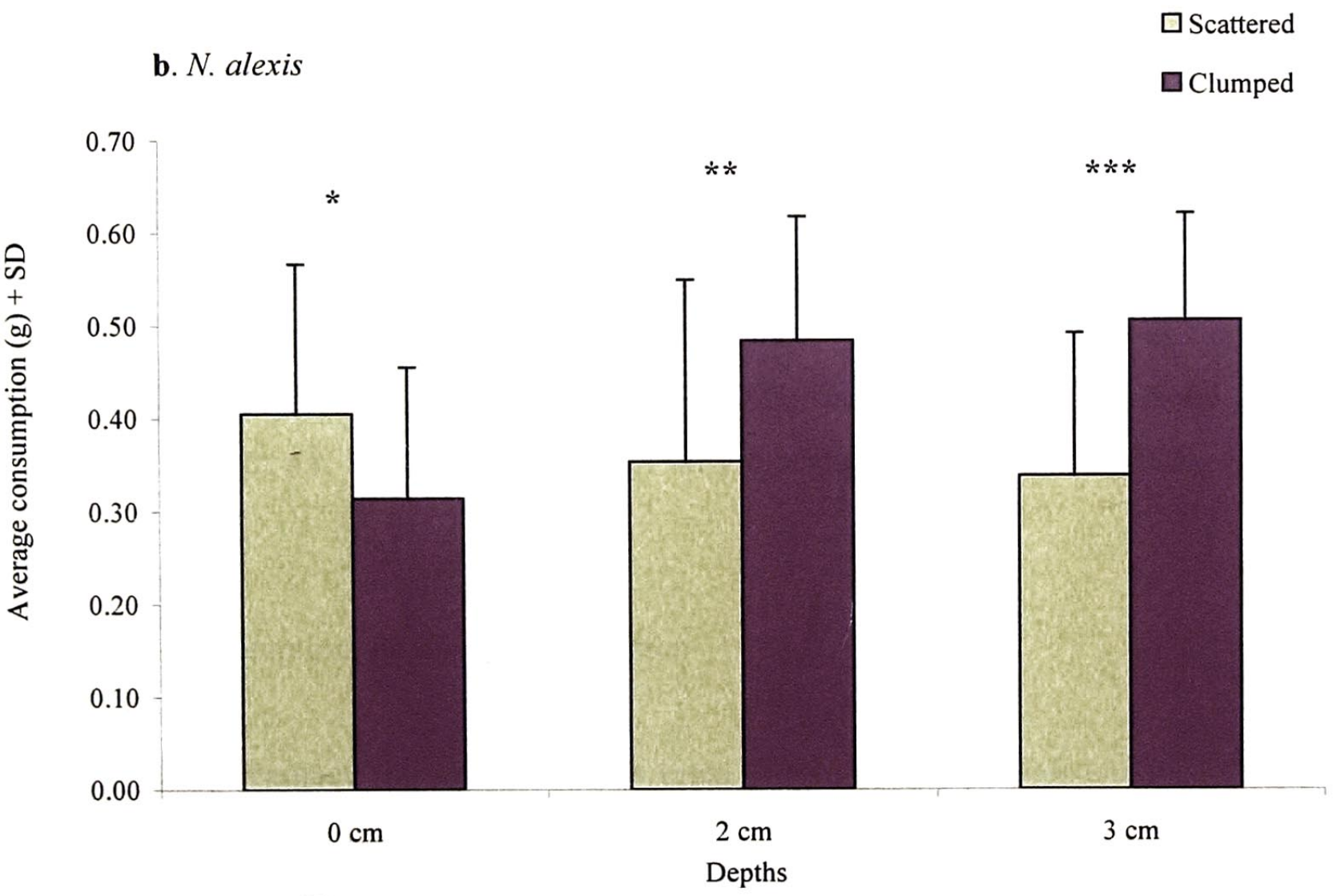


Figure 7.1. Mean consumption per gram + standard deviation of scattered and clumped seeds at three different depths for nine *P. hermannsburgensis* (**a**) and six *N. alexis* (**b**). **P*<0.05; ***P*<0.025; ****P*<0.017. Consumption is expressed as the proportion of the mass of seeds eaten of the total mass available.

df=5, P=0.018, with a=0.025, and t=-4.812, df=5, P=0.005, with a=0.017, respectively). At 2 cm and 3 cm depths there were no significant differences (t=-0.519, df=5, P>0.05). Moreover, *N. alexis* exhibited a pattern of seed exploitation similar to *P. hermannsburgensis*, with a decrease in consumption with depth in the scattered distributions and an increase in consumption with depth in the clumped distributions (Figure 7.1**b**). In particular, this species consumed a greater mass of seed in the scattered than in the clumped dispersion when seeds were on the surface (41% versus 31%, t=2.859, df=5, P=0.035, with a=0.05). When the seeds were buried 2 cm and 3 cm deep the pattern was opposite, with more consumption in the clumped than scattered distributions (48% versus 35%, t=3.510, df=5, P=0.017, with a=0.025, and 50% versus 34%, t=5.692, df=5, P=0.002, with a=0.017, respectively). The average number of clumps recovered in the clumped distribution decreased slightly with depth (3.67 at 0 cm, 3.50 at 2 cm, and 3.33 at 3 cm). *Notomys alexis* tended to eat larger seeds at greater depths in the scattered dispersion (0.04 ± 0.003 g/seed SD at 0 cm, 0.05 ± 0.004 g/seed SD at 2 cm, and 0.05 ± 0.002 g/seed SD at 3 cm), but in the clumped dispersion it consumed smaller seeds at greater depths (0.05 ± 0.01 g/seed SD at 0 cm, 0.04 ± 0.004 g/seed SD at 2 cm and at 3 cm).

Not surprisingly, *N. alexis* consumed more seed generally than *P. hermannsburgensis* (Figure 7.2**a**, **b**). In the scattered dispersions, the consumptions by the two species were not significantly different ($F_{1,13}$=4.061, P=0.065 at 0 cm, $F_{1,13}$=4.265, P=0.059 at 2 cm, and $F_{1,13}$=5.058, P=0.042, with a=0.017, at 3 cm, Figure 7.2**a**). However, in the clumped dispersions, *N. alexis* consumed significantly more than *P. hermannsburgensis* at 2 cm and 3 cm depths ($F_{1,13}$=10.146, P=0.007, with a=0.025, and $F_{1,13}$=16.875, P=0.001, with a=0.017, respectively, Figure 7.2**b**), but not on the surface ($F_{1,13}$=1.057, P>0.05, Figure 7.2**b**).

7.3.2. Seed consumption: number of seeds eaten

When the percentage frequency of seeds eaten of those available was analysed (Table 7.1), patterns of seed exploitation by the two rodent species appeared very similar to those observed for seed mass. A small difference was that *P. hermannsburgensis* consumed more scattered seeds on the surface than at 2 cm and 3 cm depths (t=4.946, df=8, P=0.001, with a=0.017, and t=3.176, df=8, P=0.013, with a=0.025, respectively, Table 7.1). No difference in consumption was observed at 2 cm and 3 cm depths. Another difference was

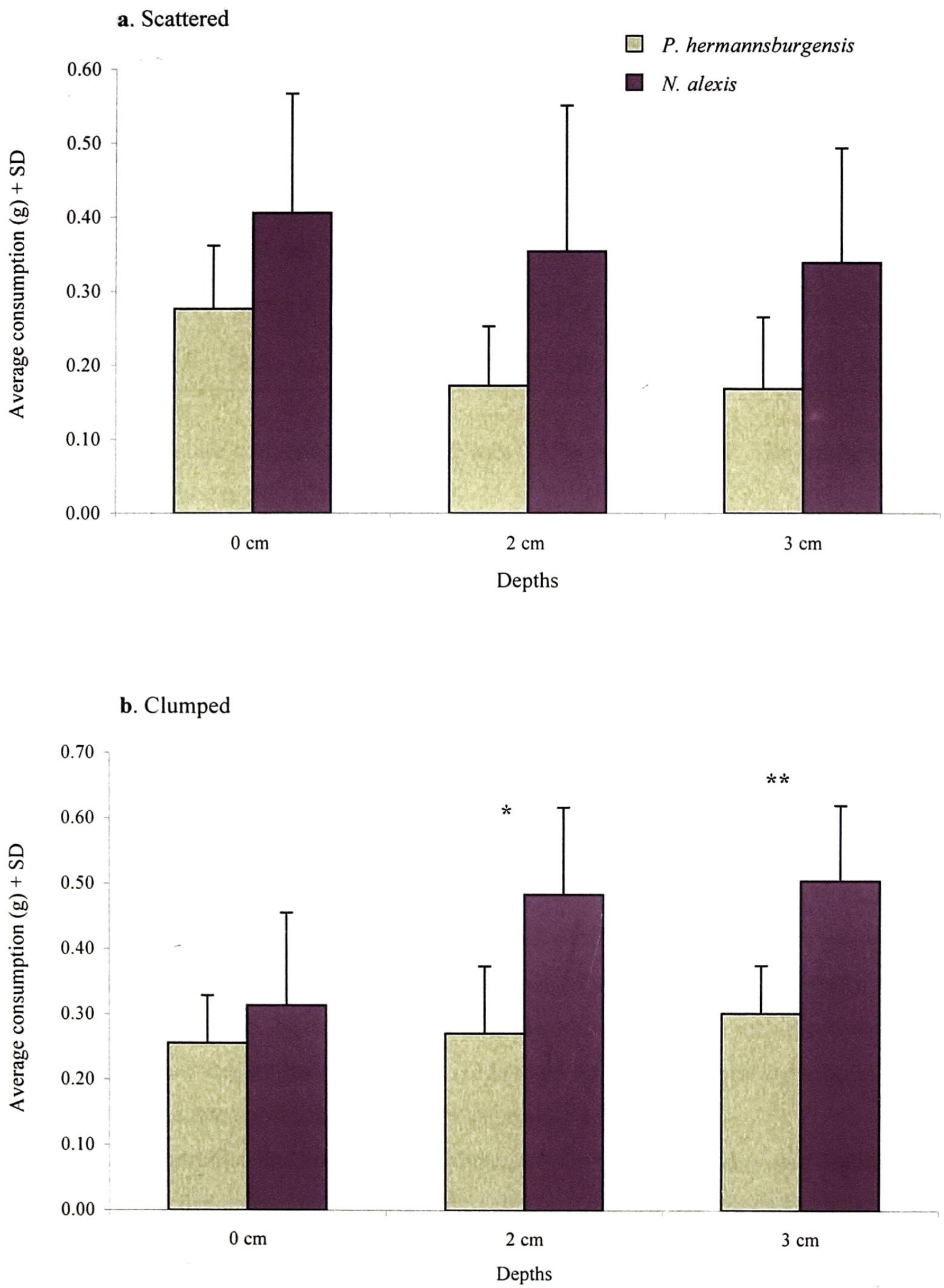


Figure 7.2. Comparison of the mean consumption per gram + standard deviation of scattered (**a**) and clumped (**b**) seeds at different depths between the two rodent species. Consumption is expressed as the proportion of the mass of seeds eaten of that available. * $P<0.025$; ** $P<0.017$. Values have been standardised by BMR of the two species.

that the percentage frequency of clumped seeds eaten by *P. hermannsburgensis* at the three depths was similar (t=-0.363, df=8, P>0.05 for 0 cm versus 2 cm, t=-2.494, df=8, P=0.037, with a=0.017, for 0 cm versus 3 cm, and t=1.113, df=8, P>0.05 for 2 cm versus 3 cm).

Table 7.1. Percentage frequency of seeds eaten of those offered to the two study species ± standard deviation for different depths and dispersions.

	P. hermannsburgensis			***N. alexis***		
	0 cm	**2 cm**	**3 cm**	**0 cm**	**2 cm**	**3 cm**
Scattered	37.1 ± 11.4	19.0 ± 9.3	18.5 ± 10.8	49.5 ± 21.9	39.3 ± 24.6	38.1 ± 19.1
Clumped	32.6 ± 8.5	33.8 ± 13.6	36.9 ± 10.8	36.2 ± 20.4	58.1 ± 19.7	59.7 ± 16.3

The average moisture contained in the sand was 0.23% ± 0.036% SD. The sunflower seeds contained 6.80% ± 0.19% SD free water.

7.4. Discussion

The results of this chapter demonstrate that seeds in clumped and scattered dispersions are exploited in different ways by the two study species. When seeds were on the surface, both species tended to consume more scattered than clumped seeds. When seeds were buried at 2 cm and 3 cm, the two rodent species exploited clumped seeds more efficiently than scattered seeds. In addition, the detection of seeds tended to decrease with depth for scattered dispersions and increased with depth for clumped dispersions, although *N. alexis* showed an equal ability to exploit seeds at the three different depths when scattered. *Notomys alexis* consumed more seed than *P. hermannsburgensis,* but the difference in consumption increased with depth in the clumped dispersion, showing that the former species is better able to exploit buried clumped seeds than the latter. The null hypothesis is therefore rejected; the two species do not have equal access to all seeds.

These results contradict the findings of McNaught (1994) that *N. alexis* was equally able to exploit seed presented in different seed distributions, and that the ability of this species in detecting seed decreased with depth, particularly if the seeds were clumped. Moreover according to 'the clump size selection' hypothesis, *N. alexis* should select clumped seeds versus scattered seeds even on the surface, while in fact the opposite pattern was observed. In this case *N. alexis* did not seem to select seeds on the basis of minimising the harvesting time and the costs involved with searching for food.

An explanation for the contradiction between results may be that differences occurred because of the test seed species used. McNaught (1994) used millet in her experiments, a much smaller seed than the sunflower seed used in this study. The mean largest linear dimension (LLD) of sunflower is three times bigger than millet's LLD, and its mean mass seven times heavier than millet (Murray and Dickman 1994b). It is likely that due to these differences the rodents perceived the latter seed species in a different way, with the harvesting rate and the costs associated with its exploitation being quite different. A larger seed species may be easier to detect even at greater depths. In addition, McNaught (1994) used only two depths (2 cm and 3 cm), thus missing the opportunity to compare the results with seed consumption on the surface. As was observed in this study, the largest differences occurred between exploitation of seed at 0 cm and the two greater depths, with little difference observed between the 2 cm and 3 cm depths. It is also likely that McNaught (1994) was unable to detect major differences between the two dispersions for this reason. The fact that animals appeared to consume more seed in McNaught's study in comparison to this one (Table 7.2), may be explained by the fact that millet seeds have been shown to be preferred over sunflower seeds in seed selection experiments (Murray and Dickman 1994b). Personal observations at the end of the present experiments showed that rodents did not always consume seeds that they had detected and recovered from greater depths. As a further point of difference, McNaught (1994) did not correct her final results for water loss and gain during trials.

Table 7.2. Comparison of mass of seeds consumed in scattered and clumped dispersions at different depths by *N. alexis* by McNaught (1994) and this study. Mean mass is shown in g ± SD.

Dispersions and depths	**McNaught (1994)**	**This study**
Scattered 2 cm	2.79 ± 0.39	1.42 ± 0.79
Scattered 3 cm	2.49 ± 0.66	1.36 ± 0.62
Clumped 2 cm	2.81 ± 0.29	1.95 ± 0.54
Clumped 3 cm	2.02 ± 0.63	2.03 ± 0.46

In contrast to North American heteromyids (Reichman and Price 1993, Price *et al.* 2000), Australian rodents do not store seeds in cheek pouches, do not cache seeds, and eat seeds one at a time. Seed clumps can thus be exploited more efficiently by heteromyid rodents, which are able to store 2-3 g of seeds in cheek pouches (Reichman and Price 1993). Since Australian rodents do not have equivalent seed storage abilities, they might not derive much greater benefit from foraging on clumped versus scattered seeds on the

surface. Moreover, if a rodent is faced with a variety of dispersions of a large seed, it is probable that the effect of dispersion differences is reduced. Even when scattered, a large seed represents a profitable, clumped resource with a substantial reward, especially in a small arena (Frye and Rosenzweig 1980). Nevertheless, the results were reversed at greater depths, where the clumped seeds were apparently more profitable or detectable than scattered seeds by the two Australian species.

It is thought that North American rodents detect seeds by olfaction down to depths of 20 cm (Howard and Cole 1967, Lockard and Lockard 1971, Johnson and Jorgensen 1981, Randall 1993, Vander Wall 1993, 1995b, 1998), and that detection improves with increasing moisture content of seeds and soil. The stock seeds used in the experiments had an average free water content of 6.8 % while the average moisture contained in the sand was 0.23%. Vander Wall (1993) observed that yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*) could not detect caches of seeds by olfaction below a certain threshold of water content in the seed (6.8 %), when the water content of the sand substrate was 0.051%. Johnson and Jorgensen (1981) showed that when soil moisture increased from 0.0092 g water/g soil to 0.280 g water/g soil, deer mice and Great Basin pocket mice (*Perognathus parvus*) found more buried seed caches. Seeds are highly hygroscopic and rapidly absorb water from the surrounding environment (Vander Wall 1993, 1998). It is probable that the seeds I tested absorbed some water from the sand when buried, and that this increased their moisture during the experiments and hence enhanced their chance of being detected by the mice.

It is also likely that the acuity of olfaction is different between species, and that the threshold changes from species to species. The results of this study showed that *N. alexis* could readily detect single seeds at 2 cm and 3 cm depths, unlike *P. hermannsburgensis*. It is therefore likely that the former species has a higher acuity of olfaction. However, Vander Wall (1998) refuted the idea of a threshold on the basis of his field results, and suggested that causes other than just the water content of seeds can play a role in their detection. During dry conditions, rodents might employ a memory-based system of cache management and then switch to an olfactory-based system during moist conditions. Nevertheless, buried seed clumps are probably more easily detected than single seeds for an olfactory-based forager, as the smell is enhanced by the quantity of moist seeds. For this reason it was easier for the two species to detect clumped seeds versus scattered seeds buried at 2 cm and 3 cm. Moreover, the two species usually consumed larger seeds in the scattered dispersion when depth increased. This may be because the larger seeds were

more easily detected than smaller seeds through releasing a stronger odour. Another explanation for choosing the larger seeds is that the rodents tried to maximise their energy intake after digging. According to this scenario, it is possible that the rodents first dug out all the detectable seeds and then selected and consumed the most profitable ones. This hypothesis is attractive, but it is unlikely to maximise rate of energy intake. Moreover, it does not seem feasible for animals that do not cache and consume their food on the spot. The differences between the two species in detecting seeds at greater depths may also be due to differences in the way the two species search for buried seeds. As hypothesised by Reichman and Oberstein (1977), bipedal rodents are facilitated in their detection ability by their more rapid movements, which allow them to discern sharp contrasts in odour.

Reichman and Roberts (1994) proposed a model of foraging in relation to seed distributions for three heteromyid rodent species. They suggested that under natural distributions and densities, the patch densities of seeds at which the minimum amount of time was required to garner one day's energy requirements differed between the three species. They found a positive relationship between the size of the rodent and the optimum patch density. The optimum minimum patch density was lowest for the smallest species and highest for the largest species. According to their model, larger species feed on high-density patches and depart before consuming all the seeds, leaving a patch density that is acceptable to the smaller species. Morgan and Price (1992) observed further that the efficiency of scratch-digging is generally greater in small quadrupedal species than in large bipedal species, and for this reason the latter should specialise on richer food patches, in the form of dense seed patches (clumped dispersions). These findings agree with previous studies of microhabitat use of the two species in the present study (Predavec 1994b, McNaught 1994). The small, quadrupedal *P. hermannsburgensis* generally forages under shrubs and bushes, largely in spinifex hummocks, where seeds are mainly scattered. The larger, bipedal *N. alexis* forages in open areas, rich in depressions and clumped seeds. It is therefore probable that the two species have developed different acuities of olfaction based on their foraging behaviours. When a forager exploits scattered dispersions it is less likely to need a strong sense of smell compared to a forager that has to find clumped resources spread over large areas. However, both species still consumed more scattered than clumped seeds on the sand surface, presumably because the cost of search for big scattered seeds, especially when caching is not utilised, is minor compared to the search for clumped seeds. Moreover, as suggested above, single sunflower seeds represent a favorable clumped resource. Instead, finding buried scattered seeds is not so immediate, and it can mean

digging haphazardly with high costs if seeds cannot be detected by olfaction. For this reason, the two species, especially *P. hermannsburgensis*, showed reduced ability to detect scattered seeds at 2 and 3 cm depths. Despite the differences in consumption of clumped seeds, the two species showed generally similar patterns of detection and exploitation of seeds. *Notomys alexis* and *P. hermannsburgensis* seemed opportunistic in their foraging, utilising seeds with the minimum search and handling time. However, in order to address this topic further, different seed dispersions should be presented to the rodents at the same time.

The results of this study suggest that the number of clumps detected decreased with depth, even if consumption increased once clumps were found. Moreover, if only consumption is considered in the analyses it is possible that the real pattern of detection would be masked. For example, the actual ability of rodents to detect seeds could really decrease with depth, but the time and energy spent in searching and digging may be compensated by enhanced consumption. Future experimental designs need to reconsider the importance of marking seed clumps in order to assess the rate of recovery of buried seeds by mice. Moreover, it would be more realistic to present different dispersions to mice together and not separately to mimic better the situation in their natural habitat. The use of clumps of different sizes is also critical to understand better the pattern of detection and selection by mice. In addition, Price (1983a) noted that results could differ with the size of the experimental arena. McNaught (1994) also found that *N. alexis* ate relatively fewer seeds in a large arena than in a small one. Results from a small arena may be biased by the spatial perception of the animals. Distances between scattered or clumped seeds may not be so large as to justify certain behaviours or patterns as found in the field, especially for fast, bipedal rodents.

7.5. Conclusions

The two species showed similar patterns of detection and exploitation of sunflower seeds provided in different dispersions. When seeds were scattered on the surface, they were exploited more than when clumped. The ability to detect clumped seeds improved with depth, while the detection of scattered seeds was reduced with depth for both species. Olfaction is probably the main means of seed detection. *Notomys alexis* probably has a higher acuity of olfaction than *P. hermannsburgensis*. Animals seemed opportunistic in their exploitation of the two types of seed dispersion at three different depths. Different

experimental designs are needed to address more clearly the behaviour of the study rodents and their adaptations to exploiting spatially patchy food resources.

Efficient exploitation of seeds and other food resources is crucial for providing sufficient energy and nutrients for growth and reproduction in desert rodents. In the next chapter, I explore the importance of one abundant seed species, spinifex, in affecting the reproductive performance of *P. hermannsburgensis*.

CHAPTER 8: THE IMPORTANCE OF DIETARY SPINIFEX SEED IN THE REPRODUCTIVE SUCCESS OF *PSEUDOMYS HERMANNSBURGENSIS*

8.1. Introduction

Outbreaks of rodents occur when there is greatly increased breeding and survival of juveniles (Newsome and Corbett 1975, Pefaur *et al.* 1979, Mutze 1989, 1991, Mutze *et al.* 1990, Twigg and Kay 1994, Dickman *et al.* 1999, Meserve *et al.* 1999, 2001). Reproduction is the most energetically demanding period in the life of female mammals (Bronson 1989). Energy expenditure during lactation is very high (Kenagy 1987, 1989, McClure 1987, Hayes *et al.* 1992, Thompson 1992), but varies within and between species depending on both life-history and environmental constraints (McClure 1987, Künkele and Trillmich 1997). Environmental constraints associated with availability and quality of food during pregnancy may slow down the acceleration in energy expenditure, typical of reproduction, and in turn negatively affect the reproductive success of small mammals (Veloso and Bozinovic 2000). Pennycuik and Reisner (1989) demonstrated further that when food is scarce, the major factor limiting population growth is the high mortality of the young.

In deserts the breeding response of rodents to primary production initiated by rainfall can be due to the abundance of free water after rain, the nutrients mobilized by plant germination and growth (White 1993, 2002), or simply the large amount of food resources produced after rainfall that allow animals to gain weight and start the reproduction process, after months of relative food shortage. It is likely that nutrients or simply the energy-abundance of food are the main triggers of eruptions of desert rodents rather than the abundance of free water after rain. Animals adapted to detect, maximise and conserve water are unlikely to be limited by the latter for reproduction (compare Chapters 4 and 5).

In support of the nutrient limitation hypothesis, Veloso and Bozinovic (2000) fed reproductive females of a precocial rodent, *Octodon degus*, with two different diets: one of high-quality food (20% protein), the other of low-quality food (12.4% protein). They showed that the different quality foods affected the reproductive energetics of the females; high-quality food increased the resting metabolic rate of lactating *O. degus*. White (1993) suggested further that high concentrations of digestible nitrogen in seeds enable females to breed repeatedly and successfully, in turn ensuring that most young survive, grow quickly, and successfully reproduce. Bomford (1987a) observed that wild house mice in rice fields started to breed only after they had access to the milk-ripe seeds of grass weeds, peaked in

numbers when fresh milk-ripe cereal grain became available, then declined in numbers when the crop ripened and was harvested. Bomford (1987c) further confirmed with laboratory experiments the role of high protein food in the breeding success of house mice. In a field experiment where food energy was not a limiting factor and protein was supplemented, an increase in the protein content of the diet of house mice from 8% to 11% was associated with a significant increase in the proportion of females breeding (Bomford and Redhead 1987). In a study on the American white-footed mouse, *Peromyscus leucopus*, Merson and Kirkpatrick (1981) fed animals on diets containing four different protein contents. They showed that a female mouse's capacity to breed was quickly and greatly reduced when dietary protein was reduced by such a small amount, or for such a short time, that it had no measurable effect on her physical condition. Finally, Allen and Hume (1997) demonstrated that the higher content of essential amino acids in green, ripening seeds than in ripe ones facilitated the extraction of more of these acids and enhanced breeding success in Zebra Finches.

In support of the energy-abundance hypothesis Bomford (1987b) supplemented wild house mice with diets of different nutritional quality, and found that the mice were limited by food supply and probably by supply of energy, rather than specific nutrients. Day *et al.* (2002) found that pregnant self-selecting Siberian hamsters, when offered three diets of different macronutrient composition, ate more carbohydrate and less fat and hoarded less carbohydrate and more fat than their virgin counterparts. By doing so, they significantly and impressively exaggerated the pregnancy- and lactation-induced increases in kilojoules eaten and hoarded. Protein intake during pregnancy and lactation did not change, as previously found in another study on Syrian hamsters (Fleming and Miceli 1983). However, laboratory rats, despite not changing protein intake during pregnancy (Richter and Barelare 1938, Leshner *et al.* 1972, Dial and Avery 1991), significantly increase it during lactation (Richter and Barelare 1938, Leshner *et al.* 1972).

These findings suggest that the quality rather than the quantity of seed is more likely to stimulate breeding in rodents. More precisely, it is not simply the amount of seed present that is important, nor the amount of nitrogen within the seeds, but the proportion of this nitrogen that is available in soluble form as one or more essential amino acids (White 2002). If this is so, an increased abundance of seeds and the consequent increase in protein abundance may maintain adult mice, but only the extra availability of soluble nitrogen in germinating and green seeds will sustain their breeding (White 2001, 2002).

It is often suggested that breeding in small mammals can be triggered or stimulated by the presence of chemicals present in green food (Reichman and Van de Graaff 1975, Negus and Berger 1977, Negus *et al.* 1977, Swanpoel 1980, Lam 1983, Nelson *et al.* 1983, Alibhai 1985). Olsen (1981) found that gibberellic acid-3 (GA_3) stimulated breeding in captive mice if added to their drinking water. Milk-ripe cereal grains and grass seeds are rich in this chemical that instead is absent or inactive in mature seeds (Murakami 1960, Stoddart 1965, Mounla and Michael 1973, Osada *et al.* 1973, Jones and Stoddart 1977, Graebe and Ropers 1978, Kurogochi *et al.* 1979).

Other factors have been found to affect the reproductive performance of house mice: temperature (Pennycuik 1972a, b, 1973, Barnett *et al.* 1975, Bronson 1979, Pryor and Bronson 1981, McAllan *et al.* 2003), social effects (Rowe *et al.* 1964, Lidicker 1965, 1976, De Long 1967, 1978, Lloyd and Christian 1969, Vandenbergh *et al.* 1972, Krebs 2003), energetic intake (Bronson 1979, Bomford 1987b, Speakman *et al.* 2001, Day *et al.* 2002), and fat content of food (Guo and Jen 1995). Photoperiod appears unimportant in controlling breeding (Bronson 1979, Pryor and Bronson 1981), and house mice in the wild are capable of reproduction at any time of the year.

8.1.1. Litter sex ratio

Sex ratios of rodent litters may be potentially influenced by maternal nutrition, and may in turn contribute to differences in rates of increase under favourable conditions. Sex-biased parental investment has been of great interest to evolutionary biologists (Hardy 2002). Several models predict sex-allocation shifts in response to variation in spatial or parental resources (Trivers and Willard 1973, Hoogland 1981, Clutton-Brock and Iason 1986). These theoretical models postulate that natural selection should favour adaptive parental control of sex allocation (Cockburn *et al.* 2002). According to Fisherian hypotheses (Fisher 1930), sex allocation should reflect the frequency-dependent advantage enjoyed by the rare sex (Cockburn *et al.* 2002). Consequently parents can usually be expected to generate an evolutionarily stable sex ratio, where the investment in males and females is approximately equal, and respond to a low number of one sex by producing more of the rarer sex. In contrast, Trivers and Willard (1973) advanced the hypothesis that in species where reproductive success varies more largely in males than in females, and where parental investment influences the reproductive success of their offspring, mothers should invest in males when they are in good body condition and in females when they are

in poor body condition. Differential parental investment in the two sexes can be achieved either by skewing the sex ratio at birth (Trivers and Willard 1973) or by diverting more resources to individual sons than daughters (Maynard Smith 1980). Males are usually larger than females at birth in polygynous species and their growth rate is faster than that of females. This suggests that males are more costly to produce and raise than females (Kovacs and Lavigne 1986, Trillmich 1986, Anderson and Fedak 1987, Boyd and McCann 1989).

Although mammalian sex ratios tend to be equal, as predicted by the Fisherian hypothesis (Clutton-Brock and Iason 1986, Cockburn *et al.* 2002, West and Sheldon 2002, Holleley 2003), there are many examples of mammals in which larger females with good body condition tend to produce more males than females (Clutton–Brock *et al.* 1982, 1984, 1986, Austad and Sunquist 1986, Anderson and Fedak 1987, Arnbom *et al.* 1994, Lamb and van Aarde 2001, Cockburn *et al.* 2002, Rosenfeld *et al.* 2003). Polygynous males are competitive and gain advantage from their larger mass and size, having greater reproductive opportunities (Clutton-Brock *et al.* 1982, Granjon and Duplantier 1993). Polygynous females instead have a relatively equal (and limited) number of reproductive opportunities, irrespective of their size or fitness (Lamb and van Aarde 2001). Lamb and van Aarde (2001) demonstrated that mice on different protein diets (20%, 15% and 10%) invested differentially in their offspring, with the mothers on the high (20%) protein diet producing more males than females as Trivers and Willard (1973) hypothesised. These mothers were also larger. No significant differences in litter size and mass and time of breeding were observed between different diets. Other studies have confirmed that sex ratio is controlled by the quality of diet, and females on low-quality diets or decreased ratios of Na, and K, to Ca, and Mg produced more females than males (Jayashree and Chowdhury 1989, Meikle and Thornton 1995, Meikle *et al.* 1995, Rosenfeld *et al.* 2003). Moreover, Meikle *et al.* (1995) found that males born to undernourished mothers were unattractive to oestrous females that preferred the odours of sons of well-nourished females and heavier males.

8.1.2. Cannibalism

A further factor potentially influencing reproduction and rate of increase in rodent populations, and which is in turn influenced by the quantity or quality of available food, is cannibalism.

Cannibalism is a widespread phenomenon in populations of animals, including mammals (White 1993). Polis (1980) defined it as a density-dependent self-regulating mechanism that maintains a population below a certain maximum size that it would otherwise reach if the animals consumed all the food that was accessible to them. On the contrary, White (1993) proposed that cannibalism evolved under the selective pressure of a shortage of protein, and hence that it is a mechanism ensuring that individuals use their food supply as efficiently as possible. He argued that the often-observed cannibalism of females eating their own still-dependent offspring under food shortage must be interpreted not as a density-dependent self-regulating process (cf. Fox 1975, Polis 1981, 1988), but as a strategy to sequester as much of the limited amount of nitrogen accessible in the environment, in order to convert it successively into the maximum possible number of offspring in the next generation.

Cannibalism is observed frequently in captive rodents (Elwood and Ostermeyer, 1984, Marsteller and Lynch 1987, Perrigo 1987, Schneider and Wade 1989, 1991, Calamandrei *et al.*1992, Wang et al. 1992, Choudhary *et al.* 1994, Khokhar *et al.* 1995, Carter *et al.* 2002, Day *et al.* 2002). Different causes trigger a cannibalistic response. Territoriality among females can induce a female to kill primarily the litters of nearby neighbours, in order to remove the closest intraspecific competitors (Tuomi *et al.* 1997, Krebs 2003). Disturbance of the nest was observed to stimulate females of the Indian mole rat, *Bandicota bengalensis*, and to enhance their cannibalistic tendencies (Khokhar *et al.* 1995). Some chemicals and hormones in the diet can enhance or in turn suppress cannibalistic behaviour (Calamandrei *et al.* 1992, Wang *et al.* 1992, Choudhary *et al.* 1994, Carter *et al.* 2002). In other cases, if females are short of metabolic energy they can modify their litter size through cannibalism on days 1-7 (or later) postpartum. The number of young eaten is expected to be a function of the total supply of metabolic energy as determined by both food supply and body fat content (Schneider and Wade 1989, 1991, Cockburn *et al.* 2002). Day *et al.* (2002) found that only Siberian hamster females fed on pellet chow cannibalised a high proportion of their pups, while females that could select their own diet among a range of food items did not demonstrate cannibalism. In fact, the former females were unable to improve their energetic state by selecting high-quality foods and, presumably, were in a negative energy balance during pregnancy and lactation. Thus, mothers recouped some of their maternal energy investment in their young by using them as a food source and also by decreasing future energy losses through continued lactation (Day *et al.* 2002).

Schneider and Wade (1989) found that the degree of cannibalism in Syrian hamsters depended on the body fat level of the mother at parturition.

When cannibalism is a function of energy availability, a decrease in ambient temperature can also trigger this behaviour (Marsteller and Lynch 1987, Schneider and Wade 1991). Food deprivation is the main cause of cannibalism in house mice during lactation (Marsteller and Lynch 1987, Perrigo 1987), with females tending to kill a limited number of pups and to continue until a sustainable litter size is achieved. Elwood and Ostermeyer (1984) studied cannibalism in male Mongolian gerbils (*Meriones unguiculatus*) and observed that males are normally not cannibalistic when cohabitating with their pregnant mates. Males instead utilise non-kin pups as food and avoid harming their own offspring. Lactation, not gestation, is the most energy-demanding period during the reproductive cycle for rodents (Racey and Speakman 1987, König *et al.* 1988, Veloso and Bozinovic 2000). Kenagy (1987) observed that females allocate energy to reproduction almost exclusively by increasing food intake that provides the primary source of energy for lactation (Rogowitz and McClure 1995). Thus energy allocated to reproduction should be influenced by food quality and quantity because these factors appear to be the most important for modulating the reproductive performance of small mammals (Veloso and Bozinovic 2000).

8.1.3. Diet and reproduction in the study species

In arid Australia, rodent eruptions are episodic and unpredictable, with rain triggering population responses on some but not all occasions. One reason for this pattern could be that grass species sometimes, for still unclear reasons, fail to set seed. Evidence for this variable response to seed pulses occurred on four occasions in the Simpson Desert study area. In 1995 plants did not respond to heavy rainfall, and no eruption of rodents was recorded (Dickman *et al.* 1999). Rodent eruptions were noted in 1991, 1992 and to a lesser extent, in 1997 when rain produced pulses of grass seeds from several species, especially spinifex.

These results suggest that spinifex (*Triodia basedowii*), the most abundant seed species produced after rain, may have a primary role in triggering desert rodent populations. In fact, from the results of Chapter 4, it is clear that this plant species is by far the most abundant in the environment, and, although it is not a preferred seed species (compare

Chapter 6), it is eaten in the natural diet (compare Chapter 4) and important during the increase phase in eruptions.

The correlation between presence of spinifex seeds and increased breeding success could be the key to explain population responses. The main idea of this chapter is that spinifex drives rodent population increases as a result of increased breeding success. I used captive breeding experiments to test the influence of spinifex seed on the reproductive success of one rodent species. I also investigate the role of spinifex in influencing sex ratios and cannibalism in *P. hermannsburgensis*. I hypothesised that animals fed, from birth, on a diet enriched with spinifex seeds, would breed sooner and either develop better offspring or more offspring than animals fed with a standard diet without spinifex seeds.

The scenario in the field is clearly more complex than this, as increase in fitness of individuals is presumably linked to several variables. Nevertheless, understanding the role that spinifex seeds play in increase or decrease of population numbers is imperative.

8.2. Materials and Methods

8.2.1. Experimental protocol and animal husbandry

I used only one rodent species in the breeding experiment, because, given the many individuals to be maintained in this investigation and the time available, it was not feasible to test both study species. The most abundant species, the sandy inland mouse *P. hermannsburgensis*, was used. The breeding experiment was conducted to determine if spinifex seed (*Triodia basedowii*) stimulates breeding. Six individuals (three females and three males) of the same stock described in the previous experiments were allowed to breed to obtain a first generation of individuals to be used. Animals were paired and their reactions and behaviour observed for a week. If the individuals were amicable, they were maintained long enough to allow them to mate. The glass aquaria used were 100 cm x 40 cm x 30 cm, filled to 4 cm deep with desert sand. Animals were kept as described in Chapter 5.

After a gestation period of 30-34 days and a suckling period of about 25-35 days, the young were removed from their mothers. Production of young in this way allowed me to obtain test animals of known age and reproductive experience. From this F_1 generation, 24 animals (twelve females and twelve males) were subsequently taken at random and separated into pairs (avoiding sibling pairs). Each pair was housed in a different cage, in

two separate rooms for the two diets to avoid possible biases caused by smell or pheromones. All 24 animals (i.e. 6 pairs in each of the two diet trials) were not run at the same time, as the production of the 24 animals from the three original pairs of wild-caught animals was staggered over about a year and a half. The experimental animals were kept under the same laboratory conditions as the stock animals. All of them were subjected to the following experimental design: two diets were offered; 1) a standard diet comprised of dry commercial seed + lettuce + mealworm or crickets for the stock and six breeding pairs, compared with 2) a standard diet with the addition of spinifex seeds for other six breeding pairs. The food was presented in plastic Petri dishes inside the glass tanks. The amount of food offered to the animals was 3.0 g for each individual as this exceeds the amount the species is expected to eat in a night (Calver *et al.* 1990, Murray and Dickman 1994b). In the standard diet 3.0 g of commercial mixed seeds for each individual were presented every night, while in the spinifex diet 1.5 g of spinifex seeds were mixed with 1.5 g of commercial seeds and offered nightly to each animal. Lettuce was provided every two nights and mealworms or crickets once a week. Six different pairs were fed each type of diet until they bred. Animals were monitored by direct inspection every day and weighed every two weeks. When the female appeared pregnant the male was removed to avoid any harm to the eventual litter. Although males were returned to their female partners after weaning (or loss) of the litters, I was not able to run the experiment for long enough to determine whether more litters were produced under one diet or the other.

8.2.2. Nutritional characteristics of the experimental diets

Table 8.1 shows a nutritional analysis of the spinifex diet compared to the commercial mixed (standard) diet offered to the two treatment groups. These nutritional characteristics were measured during the analyses of Chapter 6 and presented in the Appendix 16 (Table 14).

Table 8.1. Nutritional characteristics of the two diets offered to the mice in the breeding experiment. Mean and SD are presented for each characteristic.

Treatments	**Ash (%) ± SD**	**Energy kJ/g ± SD**	**Water content (%) ± SD**	**Dry matter (%) ± SD**	**Protein (%) ± SD**
Spinifex diet	2.0 ± 0.1	18.08 ± 0.13	8.0 ± 0.00	92.0 ± 0.00	21.38 ± 1.39
Standard diet	3.0 ± 0.5	18.96 ± 0.34	7.0 ± 0.00	93.0 ± 0.00	13.51 ± 0.89

The two diets differed most markedly in their protein content (Table 8.1)

8.2.3. Analyses

The time of breeding, the size of litters, their mass at one month, their sex ratio, and the time of weaning were compared for the two different diet treatments. The time of weaning was recorded as the first time any member of the litter was observed eating seeds. A two-sample *t*-test was used, after log-transformation, to determine any differences in litter size and time of breeding between the dietary treatments. Power analyses were performed in the statistical package GPOWER 2.0 (Faul and Erdfelder 1992) to explore the likelihood of committing type-2 errors (Quinn and Keough 2002). The sex ratio of the litters was measured as the proportion of males of the entire offspring (number of males/total offspring) and analysed with a Fisher exact test (Sokal and Rohlf 1995). Litter size and litter growth rate (as mass) were compared using Pearson product-moment correlation coefficients (Sokal and Rohlf 1995), after the data were standardised for time of record and log-transformed. The time standardisation was made by dividing the average mass of the litter by the time elapsed from their birth to the record, under the assumption that in the first period of life there is a linear relationship between growth and time (Watts 1979b).

Breeding performance of the stock pairs was compared with that of the treatment pairs.

8.3. Results

No significant differences were observed in reproductive performances of animals maintained on the two diets. There were, however, some interesting trends. The mean litter size was double for pairs on the spinifex diet compared with pairs on the standard diet (Figure 8.1). Moreover, the mean time elapsed from the formation of the pair until the birth of the litter was longer for animals on the standard diet than for animals on the spinifex diet (Figure 8.1). The result of the analysis of the difference in litter size between the two treatments was t=-0.984, df=9.8, P>0.05, while for breeding time between the two treatments t=-0.445, df=9.9, P>0.05. The small sample sizes meant that there was low power to detect any differences between the experimental treatments. A minimum number of 14 pairs would have been required to identify any effect of diet on litter size (effect size

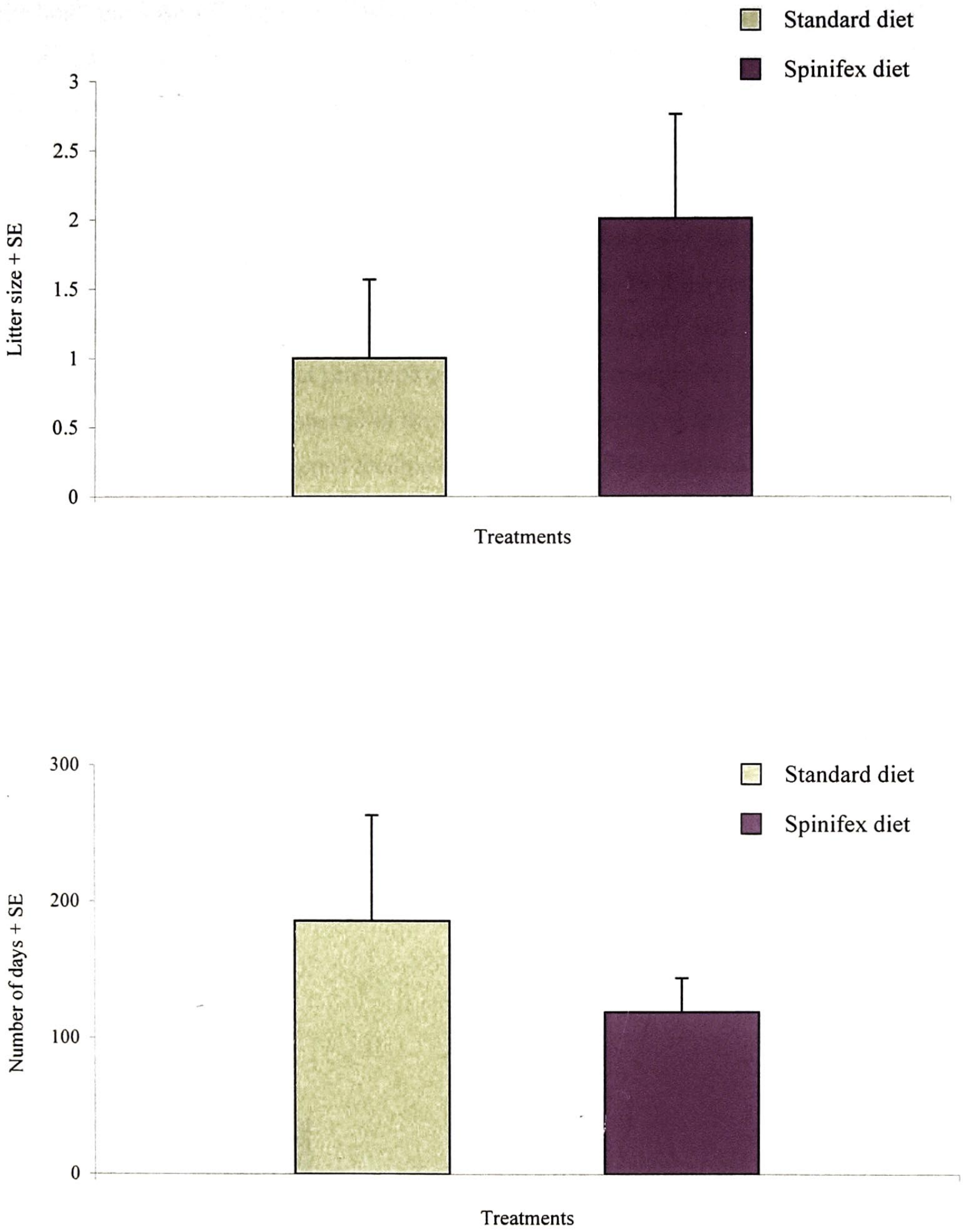


Figure 8.1 Effects of two diets, standard diet and spinifex diet, on reproduction in *P. hermannsburgensis*. In the first graph mean litter size + SE is reported for the two diets. In the second graph the mean age at first breeding + SE is reported.

d=0.674, delta=1.168, power=0.185) and at least 8 pairs to detect any effect of diet on the breeding time (effect size d=0.520, delta=0.681, power=0.087).

On the standard diet only three pairs out of six bred. Mating was observed in the other pairs and some of the females appeared to gain weight, but no pups were observed. One possible explanation is that females killed and ate them immediately after birth, and so no clear trace of the litter was left. Under the spinifex diet, four pairs out of six bred successfully. Litter survival on the standard diet was until the end of the study for two pairs, while in the third (pair 2) the mother killed the only pup at 14 days apparently because of nest disturbance. Litter survival on the spinifex diet was seriously affected by the mothers' cannibalism. All four pairs that produced young provided examples of mothers killing part of or the entire litter. This happened in the middle or at the end of the suckling period. The mother in one pair (pair 5) stopped feeding her litter after 19 day; all young died.

The mass of the litters was extremely variable. The mean growth rate per day was calculated after standardisation by time of measurement and by pooling the data on the litter masses of the two treatment groups. It tended to be negatively correlated with litter size (r=-0.814, P=0.051), even if the analysis was marginally not significant.

More female young were produced on the standard diet and more males on the spinifex diet (Fisher exact test, χ^2=8.045, df=1, P=0.013, Figure 8.2).

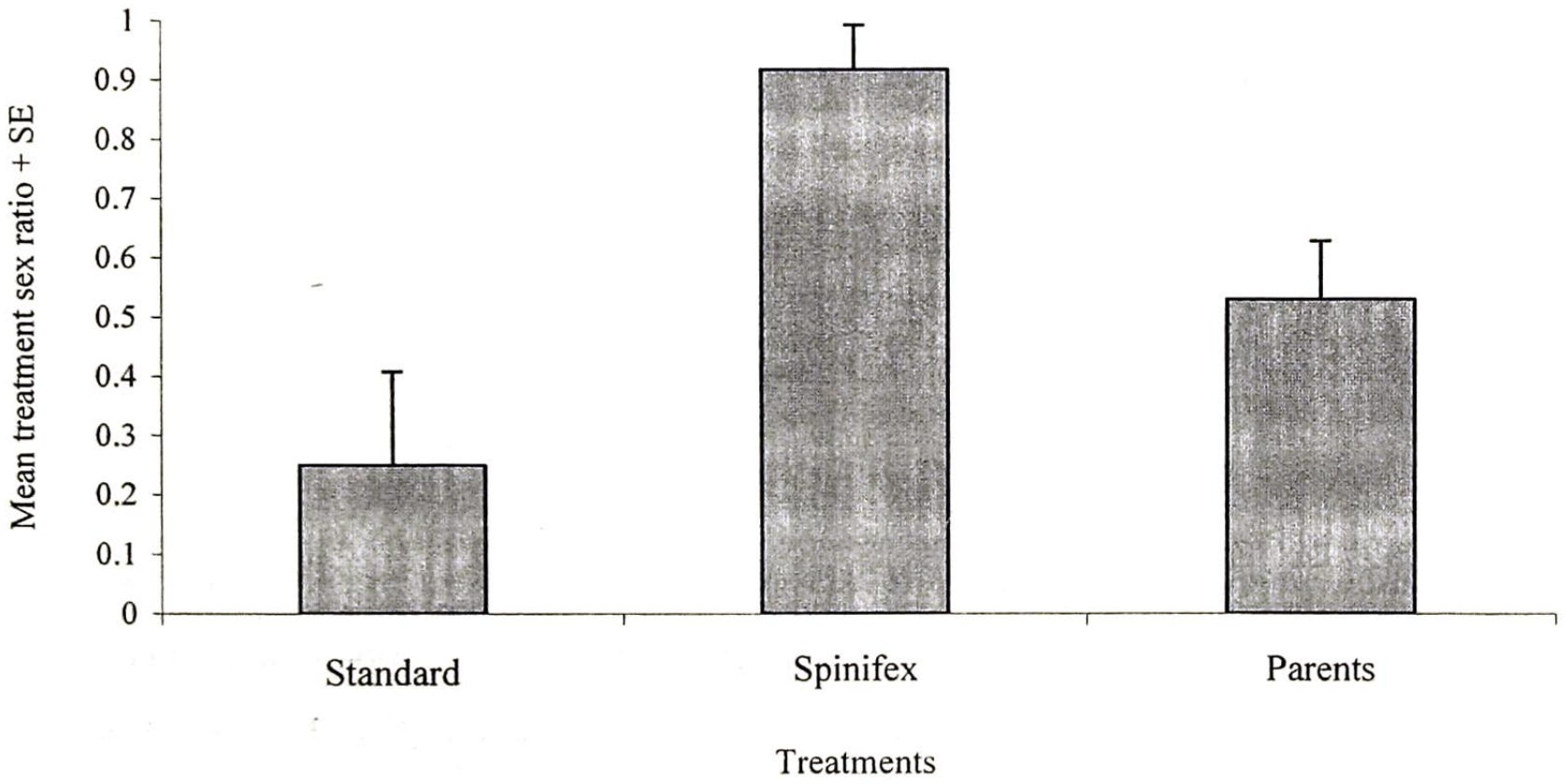


Figure 8.2. The mean sex ratios (proportion of males) of *P. hermannsburgensis* offspring produced under standard and spinifex diets, and sex ratio produced by the parental generation. Bars indicate standard error of the mean.

Despite the paucity of data, the weaning time appeared slightly longer in the spinifex diet treatment, with an average of 32 ± 2.83 SD days, compared to the standard diet treatment with an average of 26.5 ± 3.54 SD days. A summary of these results is given in Appendix 21 (Table 19).

When these results are compared with the breeding success of the stock pairs, it appears clear that the experimental pairs were less successful. The mean time taken to breed by the original pairs was 34.89 ± 9.16 SD days, compared to 186.0 ± 172.8 SD days for pairs on the standard diet, and 119.25 ± 55.72 SD days for pairs on the spinifex treatment. In this comparison, however, the age and experience of the stock pairs was not known. The mean litter size of the wild-caught animals was 2.64 ± 1.50 SD pups, compared to 1.0 ± 1.26 SD pups for the standard diet's pairs and 2.0 ± 1.67 SD pups for the spinifex diet's pairs. Litter survival for the first month was 80% for the wild-caught pairs versus 34% for the pairs on the standard diet, and 17% for the pairs on the spinifex diet. The mean growth rate of litters in grams per day was 0.251 ± 0.043 SD for the original pairs, but only 0.183 ± 0.088 SD for the pairs on the standard diet and 0.154 ± 0.029 SD for the pairs on the spinifex diet. The litter sex ratio of the wild-caught individuals tended to parity, in contrast to the skewed sex ratios produced by experimental pairs (Figure 8.2).

The mean mass of females just before pregnancy was 14.64 g ± 0.95 g SD for the original pairs, but only 12.44 g ± 0.22 g SD for females on the standard diet and 12.13 g ± 0.96 g SD for females on the spinifex diet. The mean age of females in the original pairs when they were first paired in captivity was over a year, compared with 69.0 ± 8.65 SD days for the females on the standard diet and 83.33 ± 12.23 SD days for females on the spinifex diet. The masses of litters of the original pairs were not correlated with the litter sizes (r=-0.007, P>0.05).

8.4. Discussion

The breeding experiment extended for more than two years because the time taken to breed in some pairs in the two treatment groups was much longer than expected. Moreover, the breeding success of the pairs was poor, with only some producing litters and with few litters surviving to weaning. Consequently, the paucity of data collected in this experiment makes it difficult to draw conclusions or derive robust predictions of how food affects reproductive performance. Nevertheless, some interesting patterns were revealed and they are worth further investigation. In particular, the spinifex-enriched diet seemed to have a

stimulating effect on the breeding pairs in that they tended to produce larger litters in a shorter time. The two diets differed principally in their protein content (Table 8.1). Several studies have documented the importance of protein-rich diets in the breeding success of animals (Merson and Kirkpatrick 1981, Bomford 1987a, c, Bomford and Redhead 1987, White 1993, 2001, 2002, Allen and Hume 1997). Green, ripening seeds are thought to be particularly important in stimulating, initiating and sustaining reproduction (Bomford 1987a, c, White 1993, 2002, Allen and Hume 1997) due to their higher content of essential amino acids (Sano and Kawashima 1982, Rozan *et al.* 2001) and especially gibberellic acid-3 (GA_3) (Murakami 1960, Stoddart 1965, Mounla and Michael 1973, Osada *et al.* 1973, Jones and Stoddart 1977, Graebe and Ropers 1978, Kurogochi *et al.* 1979, Olsen 1981). Interestingly, Ylönen *et al.* (2003) did not observe any effect of food quantity and quality on the breeding of house mice, and concluded that the lack of free water might have delayed and minimised the exploitation of high quality food resources that they offered. However, this should not be the case for the two study species, which are capable of exploiting food resources independently of the presence of free water (Chapter 5).

The spinifex seeds offered to the mice in the breeding experiment were mature, ripe seeds and so were unlikely to contain extra amounts of essential amino acids and gibberellic acid-3. This may explain why the first breeding events took so long to occur on the spinifex-enriched diet, although the higher protein content of the spinifex diet still may have allowed the animals on this diet to breed earlier and to produce more pups than animals on the standard diet. However, any such advantage was not sufficient to permit successful survival of the larger litters that were partially or totally cannibalised by the mothers. Perrigo (1987) found that house mice differed from deer mice in their breeding strategies. The former allowed insemination, achieved conception and attempted lactation regardless of feeding conditions, but routinely cannibalised offspring throughout the first 12 days of lactation presumably to stabilise the extra energy burden. Instead, the deer mice exhibited a rigid 'all-or-nothing' reproductive response, avoiding reproduction when the conditions were not favourable. The author proposed that these two strategies were correlated with the differential tendencies of the two species for seasonally oriented (deer mice) versus opportunistic (house mice) breeding in the wild. A similar strategy by house mice was observed by Marsteller and Lynch (1987), who found that food-restricted animals tended to cannibalise pups until a sustainable litter size was reached. *Pseudomys hermannsburgensis* is an opportunistic, aseasonal breeder in the wild, and so is likely to use the same strategy as the house mouse.

Another interesting result was the significantly different sex ratio that occurred between the two dietary treatments. Lamb and van Aarde (2001) found that multi-mammate mice (*Mastomys coucha*) fed on three diets with different protein contents showed differential maternal investment and sex-specific resource allocation. Mothers on the 20% protein diet were significantly larger than those on the lower protein diets (15% and 10%) and produced significantly more male than female offspring. Mothers on the lower protein diets did not produce sex-biased litters. These findings agreed with the hypothesis of Trivers and Willard (1973), according to which females in good body condition should invest in males, and females in poor body condition should invest in females. The findings of this chapter showed that mothers on the spinifex diet (21.38% protein) produced significantly more males than mothers on the standard diet (13.50% protein) that produced instead more females. This result may be interpreted as further evidence that the spinifex-enriched diet was more nutritionally advantageous to the mice than the standard diet, and that this was because of its higher protein content.

Mothers on the standard diet were also on average slightly larger and older at their first breeding than mothers on the spinifex diet. Although these differences were small and not tested for significance, the trends provide little support for the findings of Lamb and van Aarde (2001) that females on higher protein diets should be larger than females on lower protein diets. However, these authors also discovered that females on the high protein diet were older than females on the low protein diet when they produced their first litters. Moreover, the growth rates of the pups on the high protein diet were actually slower than those on the medium (15%) protein diet. They suggested a physiological upper limit (25% dietary protein) for responding to the positive effects of dietary protein, as already found in other species (Edozien and Switzer 1978). Van Lunen and Cole (1996) suggested that excessively low and excessively high amounts of protein intake result in a low response in growth, because at low protein: energy ratios there is a shortage of protein intake for nitrogen deposition, and at high protein: energy ratios the efficiency of tissue deposition is low because of the loss of energy for deamination and elimination of excess protein. The mean growth rate of litters in the spinifex treatment group was slightly less than that in the standard treatment group, possibly because of the higher energetic demand for metabolising the excess of protein for animals in the former group.

The correlation between litter size and litter mean growth rate in this study agrees with the findings of Kirkpatrick *et al.* (1988), who found that postnatal fraternity size (size of

litter in which an animal is reared following birth) negatively affected mass at weaning, with mice from smaller litters being heavier than those from larger litters.

Cannibalism occurred recurrently in mothers fed the spinifex-enriched diet. As explained previously, it is likely that the quality of nutrients in this diet was good enough to initiate an earlier response and to produce larger litters in smaller animals in comparison to the pairs on the standard diet, but the energy was not sufficient to sustain the lactation demands of the larger litters. Lactation, not gestation, is the most energy-demanding period during the reproductive cycle for many rodents (König *et al.* 1988, Veloso and Bozinovic 2000). Kenagy (1987) observed that the elevated food intake of lactating females is used almost exclusively for lactation (see also Rogowitz and McClure 1995). Thus, energy allocated to reproduction should be influenced by food quality and quantity, because these characteristics appear to be important factors in modulating the reproductive performance of small mammals (Veloso and Bozinovic 2000). So mothers on the spinifex diet either killed and ate part of or the entire offspring, or stopped suckling it and abandoned it. In two cases, however, this explanation is insufficient: the mothers killed and ate pups at the end of the suckling period, after a long phase of maternal investment. Some studies have shown that, during late lactation, females must ingest large quantities of energy to supply their offspring with milk, and that this period imposes the greatest energy demands on most mammals (Loudon and Racey 1987, Thompson 1992, Speakman *et al.* 2001). It is possible that the diet offered at that stage was not energetically rich enough to maintain suckling of larger pups, and that females killed and partially ate their offspring to regain energy. However, this explanation is not compelling: although cannibalism was less frequent on the standard diet, energetic demands of lactating females would still have been high due to their slightly larger body mass compared with females on the spinifex diet.

The only case of cannibalism recorded in the standard diet treatment was due to disturbance of the nest (Khokhar *et al.* 1995). A possible alternative hypothesis is that stress related to captivity had induced density dependent self-regulating behaviour in these females (Polis 1980).

The breeding success of the two diet treatment groups was less than that of the stock pairs. After their first litters, the original stock pairs produced larger litters than the two treatment groups and the time between litters was considerably shorter. Lam (1983) and Rahmini *et al.* (2003) showed that the number of preceding litters has an effect on litter size in rice-field rats in laboratory colonies, with larger litters being produced by older mothers. In other rodent species, younger females do not have the physiological maturity

to have large litters (Ingram *et al.* 1958). The age, body mass and experience of the mother have an overall effect on reproductive outcome (Singleton *et al.* 2001, McAllan *et al.* 2003). The superior breeding success of stock pairs may be due to the fact that mothers were larger and older and had already experienced their first birth in captivity. It is also likely that the first birth in captivity can be problematic and often unsuccessful even for captive-bred animals. Unfortunately, due to time constraints, the results of this chapter were limited to the first-born litters, and thus are likely to be biased by the inexperience and age of the young females.

A final caveat in discussing the reproductive results is that the nutritional analysis of the two treatment diets was quite simple and based on few characteristics. In order to be able to fully understand the pattern of reproduction and breeding success of the rodent species, more detailed analyses are needed on the composition of the diet offered. Amino acids, hormone precursors, minerals and other chemicals probably also play a role in breeding success. If some unknown chemical was present in the seeds (e.g. insecticide or fungicide) it may have influenced the reproductive success of the mice in this study in a concealed way by suppressing or enhancing their breeding and modifying reproductive behaviour. Krasowska (1989) found that an excess of fluoride caused disturbance in the reproduction of *Clethrionomys glareolus*, and that the disturbance was transmitted and enhanced in successive generations. Although such contamination is unlikely, a more comprehensive chemical analysis of treatment diets would assist in evaluating any differences that they cause in reproductive success.

8.5. Conclusions

Despite the low success of the breeding experiment of this chapter, a limited response was observed to the two diets by the mice. The spinifex diet tended to stimulate earlier breeding and larger litter size than the standard diet. It appeared that the main difference between the two diets was their protein content, with the spinifex diet being of higher quality than the standard diet and leading to a male-biased sex ratio. However, the surplus of protein in the spinifex diet, perhaps in addition to other factors, was not sufficient to permit successful survival of all litters.

In its natural habitat, *P. hermannsburgensis* probably breeds opportunistically when it is able to achieve a certain energetic or nutritional threshold, and adjusts its reproductive success (litter size, mass, weaning time) based on food availability. If the species is limited

primarily by energetic constraints it will be the quantity of food that controls its reproductive outcome. If instead the species is principally limited by nutritional constraints, it will be the quality of food that triggers its reproductive response.

Further investigations are required in order to interpret and clarify the preliminary results of this chapter.

CHAPTER 9: GENERAL DISCUSSION

9.1. Major Findings of the Thesis

Some correspondence was found between population eruptions of *N. alexis* and *P. hermannsburgensis* and the occurrence of heavy rainfall, at study sites in the Simpson Desert. In mid-1991 and in mid-1992, two eruptions were observed at Ethabuka site, following exceptional rainfall events in early 1991 and early 1992. In addition, following the extremely wet year of 2000, rodents erupted at 12 study sites in winter 2001. At different sites, rodent populations peaked with different delays and with different magnitudes after the last rainfall. However, the general pattern of eruption was similar everywhere, with population increases starting from low densities, lasting a short time, and declining again within a further six months. In contrast, in January 1995 and February 1997, large rainfall events failed to trigger population eruptions, the only exception being the small increase in *P. hermannsburgensis* in late 1997. Thus, the responses of rodents to rainfall were somewhat variable and unpredictable. The results suggested that rainfall does not directly control increases in rodent abundance, and the magnitude of the response does not always reflect the amount of rain.

Other factors clearly mediate the response of rodents to rainfall, and render it variable and unpredictable. Three models were proposed that could link rainfall to rodents:

1) *Rainfall increases availability of free water*. In desert rodents that are water-limited, the availability of free water may facilitate their increases. This did not seem to be the case in the present study, because the two species failed to respond to some heavy rainfall events. Moreover, availability of free water is short (up to about two months after rainfall), and rodent eruptions last longer than two months. In addition, rainfall is not the only source of free water in deserts, as dewy nights provide free water for 3-4 months of the year (C. R. Dickman *pers. comm.*), and rodents still did not respond to this source of free water. The results of this thesis also showed that the two species are very adept at detecting free water in their food. Finally, physiological and behavioural adaptations of the two rodent species to conserve water are very effective (MacMillen and Lee 1967, MacMillen and Lee 1970, MacMillen *et al.* 1972, McNab 1979, Dickman 1993, Predavec 1997b). Consequently, *P. hermannsburgensis* and *N. alexis* do not rely on free water in the environment to survive, and there is scant evidence that free water allows population increases or peaks. Hence, this model was rejected.

2) *Rainfall increases vegetation cover*. Increased cover may provide important shelter for rodents, allow them to escape from predation, exploit a greater range of microhabitats, and improve burrowing conditions due to the improved structural integrity of the soil with plant roots in the ground. The results showed that rain was correlated with plant cover and with plant species diversity. Moreover, capture rates of *N. alexis* and *P. hermannsburgensis* also were correlated with plant cover and species diversity, suggesting that rodents respond to rain-induced changes in abundance and variety of plant cover. However, the results also showed that the diets of both species of rodents changed over time, implying that food as well as shelter resources may be responsible for rodent number changes.

3) *Rainfall increases food availability and accessibility*. In deserts, rainfall affects primary productivity by changing vegetation composition, production and structure. Such changes are likely to directly affect rodents that are often limited by food (Newsome 1970, Boutin 1990, Predavec 1994a). New rain-induced resources should stimulate population increases. The results of this study showed that rainfall effectively increased primary productivity in the first few months after it fell, with the only exception being the plant seed bank. With regard to rodent responses to food resources, only *P. hermannsburgensis* appeared to react to changes in resources, while *N. alexis* did not show any obvious response. Rodent diet did not seem to reflect clearly the availability of food. However, the two species of rodents did change their diets during different periods of their population cycles, exhibiting differential use of foods and perhaps limiting competition for food resources. They also seemed quite selective in their diets, rather than opportunistic, avoiding some of the most common species of seeds available. The critical periods of their population cycles were probably the Increasing and Decreasing phases. During the former phase food is more abundant, and reproductive success and/or juvenile survival may increase. In the Decreasing phase, rodents may crash at low numbers without the input of new resources in the environment. The High and Low phases may be 'survival' stages of the rodent populations, during which relatively few individuals reproduce.

The two species were capable of detecting free water in their food and selected for the moistest seeds presented in captive trials. This skill should be advantageous for desert life, because the ability to maximise water intake from food allows rodents to live without free water, as previously discussed.

In captive trials, the quality of seeds appeared important to the mice. They selected some characteristics of seeds over others: protein, water content, kernel size relative to the size of the entire seed, and small dimensions. Moreover, they did not seem to be

constrained by the time necessary to process the seeds. Thus, selection criteria for seeds depended on relatively few of the measured characteristics, and were primarily nutritional and morphological. In nature the rodents may optimise their diet by choosing to ingest the most appropriate seeds amongst a vast range. Trade offs such as availability, searching time, handling time, predation risk, nutrient content, moisture, and secondary defence mechanisms of the seeds may be very important in the selection process. The fact that the rodent species selected for the same seed characteristics and that their concordance in preference was quite high, probably means that both species experienced the same constraints, and may compete in nature for the same food resources.

Seeds selected in the captive experiments appeared different from those observed in the diets of both species of rodents. Some seed species tested in laboratory experiments were not found in the gut contents of either species (e.g. *Trichodesma zeylanicum*, *Cleome viscosa*, *Cassia pleurocarpa*). Others were avoided equally in the selection experiments and in the natural diet (e.g. *Triodia basedowii*, *Eragrostis eriopoda*). However, certain seed species were avoided in the diet but selected in the experiments, or vice versa (e.g. *Trachymene glaucifolia*, *Eriachne aristidea*, *Paracteneum refractum*, *Aristida contorta*). Biases in the analyses or expression of behaviour due to captivity may explain such results.

The two species were capable of detecting and recovering seeds at depths of up to 3 cm. They also exploited scattered and clumped seeds in different ways. Superficial seeds were consumed in higher abundance if scattered than if clumped. When seeds were buried the two rodent species more readily detected clumped than scattered seeds. Detection of seeds decreased with depth for scattered seed dispersions but increased with depth for clumped dispersions. *Notomys alexis* seemed more capable of exploiting buried clumps of seeds than *P. hermannsburgensis*. Thus, the accessibility to the ground seeds seemed to be a function of the differential capabilities of detection of the two study species.

In breeding experiments, spinifex seed in the diet had a stimulating effect in that pairs of *P. hermannsburgensis* tended to produce larger litters in a shorter time. Since the two diets differed markedly only in their protein content, the results suggest that nitrogen-rich food has an important influence on the population dynamics of this species.

9.2. Interspecific Differences

Differences in capture rates between the two species and the virtual disappearance of *N. alexis* from the capture record from October 1993 until March 1998, may reflect

interspecific differences in foraging strategies and microhabitat use. The two species appeared to be selective in their diet to different degrees, reflecting food availability and perhaps interspecific competition. Dietary selectivity may be explained because, unlike heteromyids (Reichman 1977), Australian rodents do not appear to cache seeds (Dickman 1996c), and they have to maximise their nutrient and water intake per unit time on the spot. The lack of obvious dietary opportunism may contribute to depressing populations of both study species and maintaining them at very low numbers, especially during periods when the abundances and species diversity of food resources are low and the rodents do not have many foods to eat. The two species also seem to partition the available food resources during times of food scarcity. *Pseudomys hermannsburgensis* usually forages under spinifex hummocks where seed species diversity is relatively low, whereas *N. alexis* forages more in the open where food resources are richer (Murray and Dickman 1994a). Moreover, the fact that *P. hermannsburgensis* showed a significantly restricted niche breadth during the High population phase and usually had a less varied diet than *N. alexis*, may mean that the former species needs a smaller range of food items to survive than *N. alexis*. This may be advantageous during periods of drought when plant and available seed species diversity is reduced to a minimum. In addition, *N. alexis* may experience higher interspecific competition with birds, ants and other mammals in open areas than does *P. hermannsburgensis* when foraging under spinifex (Tischler 1998). *Notomys alexis* may also be more affected by predation than *P. hermannsburgensis* by using open microhabitats; this species is particularly susceptible in the open to predation from red foxes and feral cats (Mahon 1999). All these factors may explain why *P. hermannsburgensis* endures long periods of drought better than *N. alexis*.

9.3. The Role of Food in Rodent Population Dynamics

From these results it appears that rainfall stimulates changes in primary productivity, by increasing both abundance and species diversity of food resources, and shelter. Rodents do not always respond to such increases. When populations are at low density, increases in food resources and shelter after rain may improve the general condition of individuals. However, this situation may not be enough to stimulate widespread reproduction in the population and trigger eruptions. It has been found that the age and body mass of the mother have an overall effect on reproductive outcome (Singleton *et al.* 2001, McAllan *et al.* 2003). It is likely that rodents need a large amount of good quality food (nitrogen-rich

foods such as green vegetation, green seeds, fruits, invertebrates) to start and sustain their reproduction (Merson and Kirkpatrick 1981, Bomford 1987a, c, Bomford and Redhead 1987, White 1993, 2001, 2002, Allen and Hume 1997, Lamb and van Aarde 2001). Heavy rains may differentially increase cover, seed and flower production of diverse plant species, depending on the status of the soil nutrients. Nitrogen is likely to be a limiting nutrient in the diet as in soils (White 1993), especially in Australian deserts (Stafford Smith and Morton 1990). If rain occurs on depleted soil, the resulting plant production will be of reduced nutritional value (food resources will be carbon-rich since carbon is not a limiting nutrient) (White 1993). Moreover, if rain occurs after periods of intense production of green vegetation, seeds and flowers, during which all the available nitrogen has been already extracted from the soil, it may not stimulate a marked response from vegetation, and produce food of low quality (Morton and Baynes 1985, Stafford Smith and Morton 1990). Long periods are necessary to enrich the soil of limiting nutrients after their depletion. An example of this situation may be found in the present study in the lack of rodent response to the 1995 and 1997 rains, when an increase in primary productivity was evident. It is likely that the quality of food resources during these periods was not sufficient to initiate reproduction in the rodent populations. Consequently, it is important to ascertain the nutritional value of crops, and to understand that not all rain-induced food resources trigger rodent eruptions. Limitation of heavy grazing at long term may contribute to enrich the soil, and facilitate more palatable plants other than spinifex.

Pech *et al.* (2003) proposed that the rapid increase in abundance of rodents from low numbers to eruptions depended on three intrinsic factors: 1) the population density at the start of the breeding season, 2) the rate of increase over the breeding season, and 3) the duration of the breeding season. They concluded that eruptions occurred under the joint probability of high values for at least two of the three factors. The onset of breeding for mice may be controlled by access to high-quality food. However, the magnitude and the length of the response may be due to these intrinsic population characteristics that are not constant but may also be influenced by climate and food resources. Thus, even if rainfall produces adequate food resources, but rodent populations are at very low densities and food abundance and quality do not sustain a long breeding season, eruptions will not occur. Immigration and recruitment of individuals that follow rain-induced resources (Dickman *et al.* 1995) may increase the first intrinsic factor and thus facilitate onsets of eruptions, especially when densities are low and adult females less aggressive (Krebs 2003).

The decline of food resources in the environment occurs quite fast, if new inputs of rainfall do not occur (Dickman *et al.* 1999). When rodent populations are at high density, they are likely to quickly impoverish the habitat of limited food resources. Mahon (1999) found that reproduction declined at peak density or soon after in both 1991 and 1992 for both study species. Social suppressive phenomena may act at high densities, such as inhibition of reproduction (Breed 1979, Krebs 2003, Wolff 2003), territoriality (Krebs 2003, Wolff 2003), dispersal (Krebs 2003, Wolff 2003) or cannibalism and infanticide (as observed in this thesis; also Krebs 2003, Wolff 2003). Once these mechanisms are operating inside the population, even addition of good quality food would not stop a decline (Predavec 2000). Moreover, predators usually follow heavy rains and rodent population eruptions (Dickman 1996a, b, Dickman *et al.* 1999), and may be a contributing cause of population declines (Brown and Ernest 2002, Lima *et al.* 2002, Arthur and Pech 2003, Byrom 2003), together with diseases (Carstairs 1974, Munger *et al.* 1983, Feore *et al.* 1997, Begon 2003).

9.4. Population Dynamics and Models

Similar responses of these two species to rainfall have been documented previously in arid Australia (Finlayson 1939, Newsome and Corbett 1975, Carstairs 1976, Masters 1993, Predavec 1994b, Predavec and Dickman 1994, Southgate and Masters 1996, Dickman *et al.* 1999). Lack of response to some very wet periods by rodents also has been documented in arid and more temperate parts of Australia (Newsome and Corbett 1975, Saunders and Giles 1977, Dickman *et al.* 1999). Similar patterns have been observed in other arid regions of the world for rodents (Beatley 1969, Whitford 1976, Fuentes and Campusano 1985, Jimenez *et al.* 1992, Brown and Harney 1993, Meserve *et al.* 1995, Jaksic *et al.* 1997, Meserve *et al.* 1999, Lima *et al.* 1999, Brown and Ernest 2002). Many general theories, specific models and factors have been proposed to describe rodent population dynamics (e.g. Pech *et al.* 1999, 2003, Brown and Ernest 2002, Krebs 2003, Wolff 2003). Some of them stress the importance of extrinsic factors such as food abundance and quality, predation and diseases in controlling rodent population dynamics, others stress intrinsic factors. Brown and Ernest (2002) in their review on rainfall and rodents, based on long-term and short-term studies in North and South America, presented Model 3 of this thesis as a 'bottom-up' pattern of regulation where pulsed resource inputs are transmitted up food chains, producing increases first in primary productivity and then in successively higher

trophic levels. This model contrasts with 'top-down' regulation where predation by top carnivores cascades down food chains to affect successively lower trophic levels (e.g. Oksanen *et al.* 1981, Carpenter and Kitchell 1988). Brown and Ernest (2002) presented examples that encouraged acceptance of the 'bottom-up' model (e.g. Brown and Harney 1993, Shenbrot *et al.* 1994, Meserve *et al.* 1995, Kelt *et al.* 1996, Madsen and Shine 1999, Ernest *et al.* 2000), and examples that failed to sustain the model (Valone *et al.* 1995, Lima *et al.* 1999, Ernest *et al.* 2000). They concluded that, based on 23 years of study at their own study and on overall findings of their review, the 'bottom-up' model is too simplistic, and that the responses of desert consumers to precipitation are complex and nonlinear. Heavy rainfalls can cause either catastrophic declines in rodent populations (Valone *et al.* 1995) or trigger eruptions via increased food supply.

Predation may also have a nonlinear effect on rodent populations, depending on the frequency and vicinity of favourable conditions to rodents, and the type of predation involved (e.g. type 2 or type 3; Newsome and Corbett 1975, Mahon 1999). If periods of high rainfall and primary productivity occur sufficiently close together, predators that have built up as a response to the first rodent peak could inhibit or even prevent a second rodent response to favourable conditions (e.g Lima *et al.* 2002). On the other hand, if favourable conditions are separated by sufficient time, and predators have already declined, rodents could peak again under good conditions.

In his review of rodent behavioural strategies, Wolff (2003) reiterated the importance of extrinsic factors (food limitation, predation, diseases) as major causes of regulation of rodent populations, and rejected intrinsic factors such as territoriality, dispersal, reproductive suppression, and infanticide as minor causes in stabilising and regulating populations. On the contrary, Krebs (2003) affirmed that social behaviour might have a major role in affecting population density changes. Social behaviour is influenced by population density and may have a strong impact in shaping populations, especially via spacing mechanisms during eruptions. Spacing behaviour does not result just from direct physical aggression, but may also include avoidance and other direct and indirect physical interactions mediated by contact, odour or other sensory channels. For example, changes in reproductive activity of house mice do not appear to be driven by rainfall, but instead are associated with density, with populations showing high reproductive activity at low numbers and low and declining activity at peak densities (Krebs 2003). Such findings are consistent with inverse density dependent reproduction during the eruptions of the study species observed by Predavec (1994a, 1994b) and Southgate and Masters (1996).

Population fluctuations are often a consequence of dominant feedback loops caused by the food web structure where the population is embedded (Royama 1992, Stenseth *et al.* 1997, Bjørnstad *et al.*1998, 2001, Forchhammer and Åsferg 2000, Lima 2001, Lima *et al.* 2001a, b, Lima *et al.* 2002). If models to describe small mammal populations are to achieve generality, they should usually incorporate predator-prey relationships together with climatic and stochastic forces (Lima *et al.* 2002). In general, the order or number of lags related to the regulatory structure reflects the number of functionally different interacting groups (Royama 1992, Berryman 1999, Bjørnstad *et al.* 2001). Lima *et al.* (2002) presented a general, simplified feedback and density-independent model to describe small mammals and their predator population dynamics that included self regulation terms (intraspecific competition) and interspecific (trophic) effects together with the effects of climate-related density-independent factors (annual rainfall and the Southern Oscillation Index). Their results showed that the relative influence of these factors differed between species. These differences might be caused by different feedback structure (Berryman 1993, Lima 2001). In particular, two small mammal species that had relatively stable populations were shown to be regulated by first-order feedback (intraspecific competition) and limited by rainfall. This suggested that food was the limiting factor for these populations that represented granivorous-insectivorous and strictly insectivorous species, respectively. In contrast, a third species of small mammal that exhibited strong fluctuations and that was granivorous-herbivorous was regulated by first- and second-order feedback caused by predation, in addition to rainfall influences. Thus, during periods of high rainfall and consequent elevated food abundance, intraspecific competition for food in the rodent population was relaxed, while trophic interactions between rodents and predators dominated the dynamics of the species.

The role of diseases and parasites in regulating population dynamics is still essentially unknown for most species of mammals and other vertebrates (Begon 2003). However, some studies have documented their importance in the reduction of fecundity in rodents and their impact in relation to host density and cycle phase (Feore *et al.* 1997, Cavanagh *et al.* 2002, Begon 2003).

All these examples demonstrate the complexity of rodent population dynamics. Numerous factors play crucial roles in the population cycle at different stages and with different degrees of magnitude. Some effects may be interconnected and may generate cascade processes that accelerate population changes. The models proposed in this thesis appear to be too simplistic to be able to fully explain natural patterns (Brown and Ernest

2002). However, neither are they 'wrong', because the mechanistic processes that underpin them are real, as several previous studies have demonstrated (e.g. Hillel and Tadmor 1962, Rosenzweig 1968, Whitford 1976, Fuentes and Campusano 1985, Brown and Heske 1990, Brown and Harney 1993, Meserve *et al.* 1995, Madsen and Shine 1999, Ernest *et al.* 2000, Jaksic 2001, Lima *et al.* 2002). The problem of these models is their inadequacy to consistently predict the structure and dynamics of natural systems. While it may be possible in some cases to explain and understand the causes of fluctuations after they have happened, it will be almost impossible to predict future changes in most systems (Brown and Ernest 2002).

In conclusion, the link between rainfall and rodent population dynamics is still not clear. Initial extrinsic factors (such as rain-induced increases in food abundance and quality) may trigger increases in rodent numbers. At high densities intrinsic factors may be important in limiting further increases, and initiate a decline that may be accelerated by other extrinsic factors such as predation, diseases and food depletion. The nonlinear relationship between rainfall and rodent population dynamics makes perfect sense if we consider the complexity of the matrix of extrinsic and intrinsic factors that are involved in the equation. And this is also valid for my system.

9.5. Conservation and Management

The two study species have survived the mass extinction of small mammals that has eradicated approximately 40% of the original rodent and small marsupial fauna from several desert localities over the last century (Morton and Baynes 1985, Morton 1990). They are the most common rodent species in the Simpson Desert, and their distributions spread across most of arid Australia. Despite not being in serious danger of future extinction, these two rodent species inhabit a very harsh environment that makes them vulnerable during certain periods of their cycle. From the results of this thesis, it is easy to surmise that heavy predation during periods of low density may mean the extinction of rodent populations from certain areas. Introduced predators such as cats and foxes should be removed or at least reduced at critical stages of population fluctuations (Mahon 1999). The two study species are well adapted to detecting, exploiting and conserving water in their environment; this frees them from the necessity of dependence on free water, and provides a huge advantage with respect to introduced species that need free water to persist. In non-pastoral areas, artificial water supplies and sources should therefore be minimised or

removed to advantage native, desert-adapted species. Often, heavy predation happens in proximity to watercourses and bores where cats and foxes gather to survive harsh desert conditions (Gibson *et al.* 1994).

Another crucial factor to consider for the conservation and management of rodent populations in Australian deserts is the control of livestock and other introduced herbivores such as camels (*Camelus dromedaries*) and rabbits (*Oryctolagus cuniculus*). Their impact on the ecosystem is consistently detrimental, having negative effects on soil, soil crust communities and vegetation (Shephard 1999). Heavy grazing may impoverish the plant community and reduce species diversity and food quality for the rodents (Harrington *et al.* 1984, Grice and Barchia 1992). It may also decrease plant cover that is very important (as the results showed) for exploiting microhabitats, for moving between neighbouring areas, for shelter and burrowing. The massive presence of livestock in an area may compact the soil and render difficult the exploitation of the seed bank. Cattle may also have serious effects on the burrow systems of rodents, and on the integrity of the soil crust that otherwise facilitates burrowing, through trampling (Hodgins and Rogers 1997). In addition, all these animals may compete with the rodents for the best food resources such as green vegetation, green seeds, grasses etc. The presence of the rabbit may have a further indirect effect on rodent predation. In fact, the red fox and the feral cat may concentrate their activities in an area rich in rabbits on which they preferentially prey, but will shift to other food items such as rodents during drought when rabbits and other foods are scarce (Dickman *et al.* 1999). Even if more dependent on free water than native rodents (Moro and Morris 2000a, Moro 2001), the house mouse may represent another threat to desert rodent species, especially near areas of runoff, watercourses, salt lakes, and stony outcrops (Shephard 1999). When this species plagues, it may penetrate far into the desert dunefields and start to compete with the local rodents (Moro and Morris 2000b, Moro 2001). Moreover, it may be a vector of diseases and parasites (Davis and Anderson 1971, Samuel *et al.* 2001, Williams and Barker 2001).

In order to assure Australian desert rodents the best conditions to persist, these introduced species should be controlled, reduced or removed from the habitats of native rodents (Moro 2001), at least in localised areas where management could be focused. Moreover, artificial water bores and sources should be removed or limited because of their indirect effect in attracting introduced predators and competitors. A stepwise protocol for management was proposed by Dickman (1993).

Another essential aspect of desert management and conservation is habitat protection. Many extinctions of small mammals and marsupials appear to have been due to habitat loss. High plant diversity, abundance and floristic richness are important in assuring a wide range of food resources for rodents, including particular nutrients, trace elements and minerals. Fire may be a further, important aspect of habitat management. Fire has always had a vital role in increasing the supply and diversity of food for desert Aborigines (Latz 1996, Bradstock and Cohn 2002). The burning system employed by Aboriginal people produces a mosaic of plant communities in different stages of fire recovery that maximise production from different plant groups (fire tolerant and intolerant) (Stafford Smith and Morton 1990, Latz 1996). This procedure requires burning patchily over a wide area as often as possible at the end of a drought, as described by Latz (1996). This will assure a production of long-term food supplies and the necessary habitat complexity. Some plants (fire weeds) require regular burning to attain their maximum production. Latz (1996) estimated that the production of fruit by a colony of *Solanum centrale* was 20 kg during the first growth season after a bushfire, while after three years it had dropped to 0.26 kg and disappeared completely at five years after the fire. Moreover, the mosaic reduces the occurrence of intense fires over large areas that are dangerous for fire-sensitive communities such as mulga stands. The presence of large estates with grazing stock has prevented the use of this traditional practice, causing an increasing production of spinifex that proliferates in poor soils to the detriment of other plant species and some desert animals. Spinifex provides good flammable material that, after a build-up, can fuel extensive and devastating wildfires. Appropriate management of fire is essential in desert management and conservation (Bradstock and Cohn 2002). The merits of patch-burning on a local scale in spinifex grassland have been discussed by Letnic and Dickman (2003).

9.6. Conclusions and Further Directions

The results of this thesis showed that native rodents responded to rain-induced food resources in a nonlinear way. Several factors may be involved in changing rodent numbers, both extrinsic and intrinsic. Food abundance, but above all, quality seems to be a key factor in initiating rodent increases in nutrient-limited populations. During certain phases of rodent population cycles rainfall may stimulate mobilisation of nitrogen in plants through germination and production of fresh, green plant material and seeds. This phenomenon eases the assimilation of the limiting nutrient that may, in turn, stimulate reproduction and

increases in rodent population numbers. Free water did not appear to be limiting for animals that are capable of gaining sufficient water from their diet. The two species could potentially have been able to exploit all the food resources available, even seeds up to 3 cm depth in the seed bank, but they appeared to be quite selective in their diet. Possible intrinsic factors such as cannibalism and litter size reduction may also play a role in limiting and stopping population increases at high density. Differences in dietary strategies and foraging behaviour were observed between the two species. Coexistence seems to be achieved mainly by partitioning of microhabitat use, and secondarily of food resources.

This thesis was focused on the granivorous portion of the diet of the two study species. However, considering that during some periods mice consumed invertebrates for up to 50% of their diets, and that this food category is less likely to fluctuate in time than seeds, it is crucial to include this important food resource in further studies, and monitor fluctuations of invertebrate abundance and quality with respect to population fluctuations of mice.

One of the assumptions of this thesis is that Simpson Desert soil is poor in nutrients and that the lack of a response to rain by plants is often due to nutrient depletion in the soil. In future, it will be crucial to understand better the role of soil nutrients in driving and supporting desert food chains, their abundance, their fluctuation in time, and the time elapsed before complete depletion. Conversely, it will be equally important to investigate the time it takes to re-enrich the soil after depletion, to achieve mobilisation of nutrients, and the different amounts of nutrients necessary to plants during their entire cycle (from flower to seed). It will also be interesting to investigate different amounts of nutrients that may be necessary to different plant species.

Because of logistical constraints, I was not able to obtain large and representative samples of soil to get adequate information on the soil seed bank. Thus, it will be interesting to work with larger data sets of soil samples to track down the real importance of the seed bank for rodents (Price and Joyner 1997).

Further experiments on rodent reproduction could clarify the role of particular nutrients, water or other chemicals in triggering increases in numbers. Moreover, it will be interesting to test whether quantity or quality of food is most important in initiating reproduction. Diets of different quantity and quality could be offered to a first generation of captive mice to observe the results produced on the second generation. The number of replicates for dietary treatments should be high, perhaps n=10 or more per treatment per species, due to potentially high variance arising from cannibalism or other artefacts of captive husbandry.

In the field, experiments on cover removal from some areas would be useful to test the effects on the two study species and to understand to what degree model 2 of this thesis is applicable in natural conditions.

Finally, it would be intriguing to distinguish the role of parasites in driving changes in rodent population dynamics. In this thesis, parasites were noted in the diet of the study species and briefly discussed, but preliminary results showed that parasites might be related to decreases in the numbers of *N. alexis*, at least. A more careful analysis of the incidence and prevalence of parasites on a large number of samples may disclose another important factor involved in rodent population changes.

Clearly, elucidation of the many factors driving populations of desert rodents will provide an exciting challenge for researchers in future.

How many animals we have learned about for the first time in this age; how many are not known even now?
Many things that are unknown to us the people of a coming age will know.
Many discoveries are reserved for ages still to come, when memory of us will have effaced.
Our universe is a sorry little affair unless it has in it something for every age to investigate…..
This age will glimpse one of the secrets; the age which comes after us will glimpse another.

Seneca, *Naturales Quaestiones*, I century

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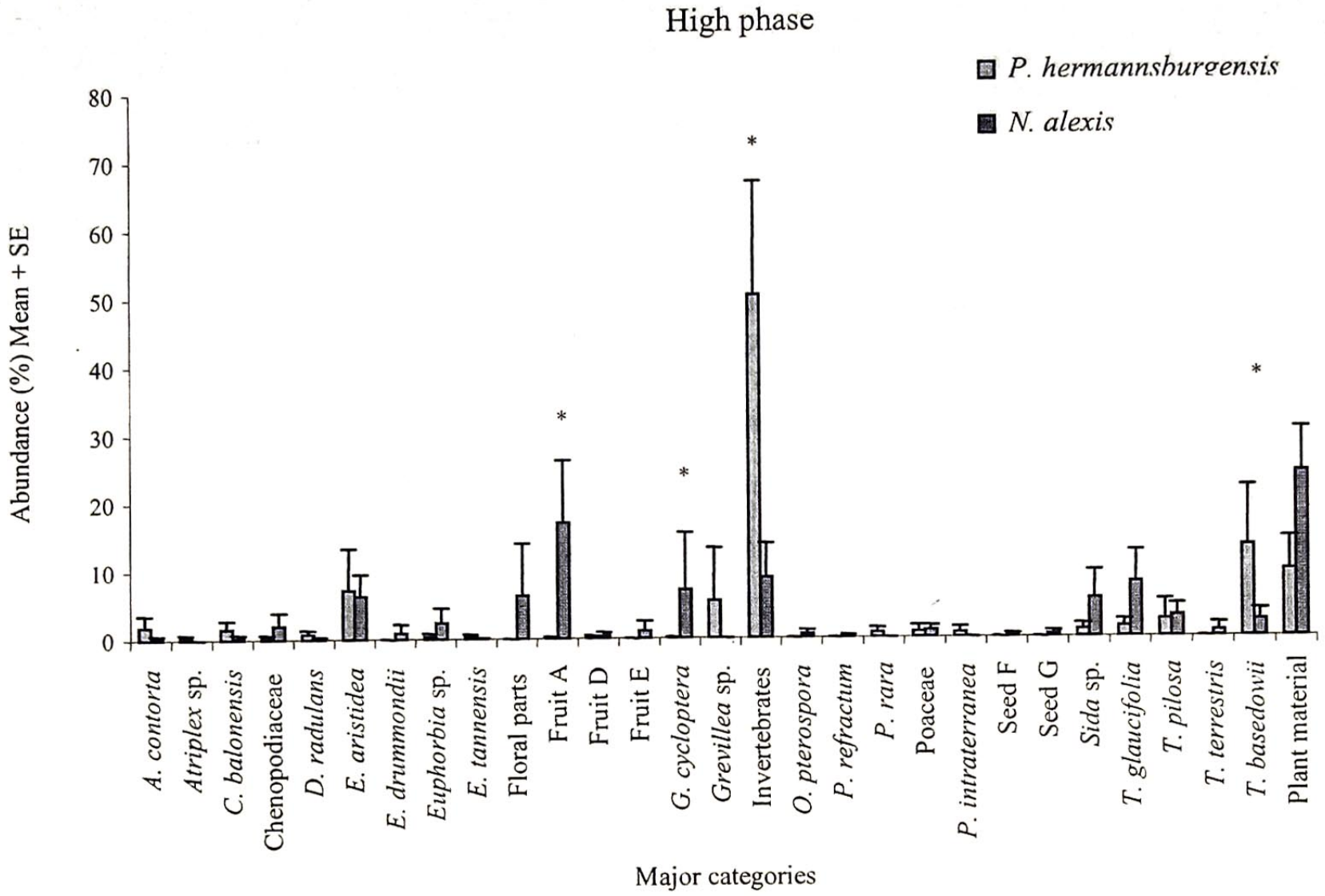

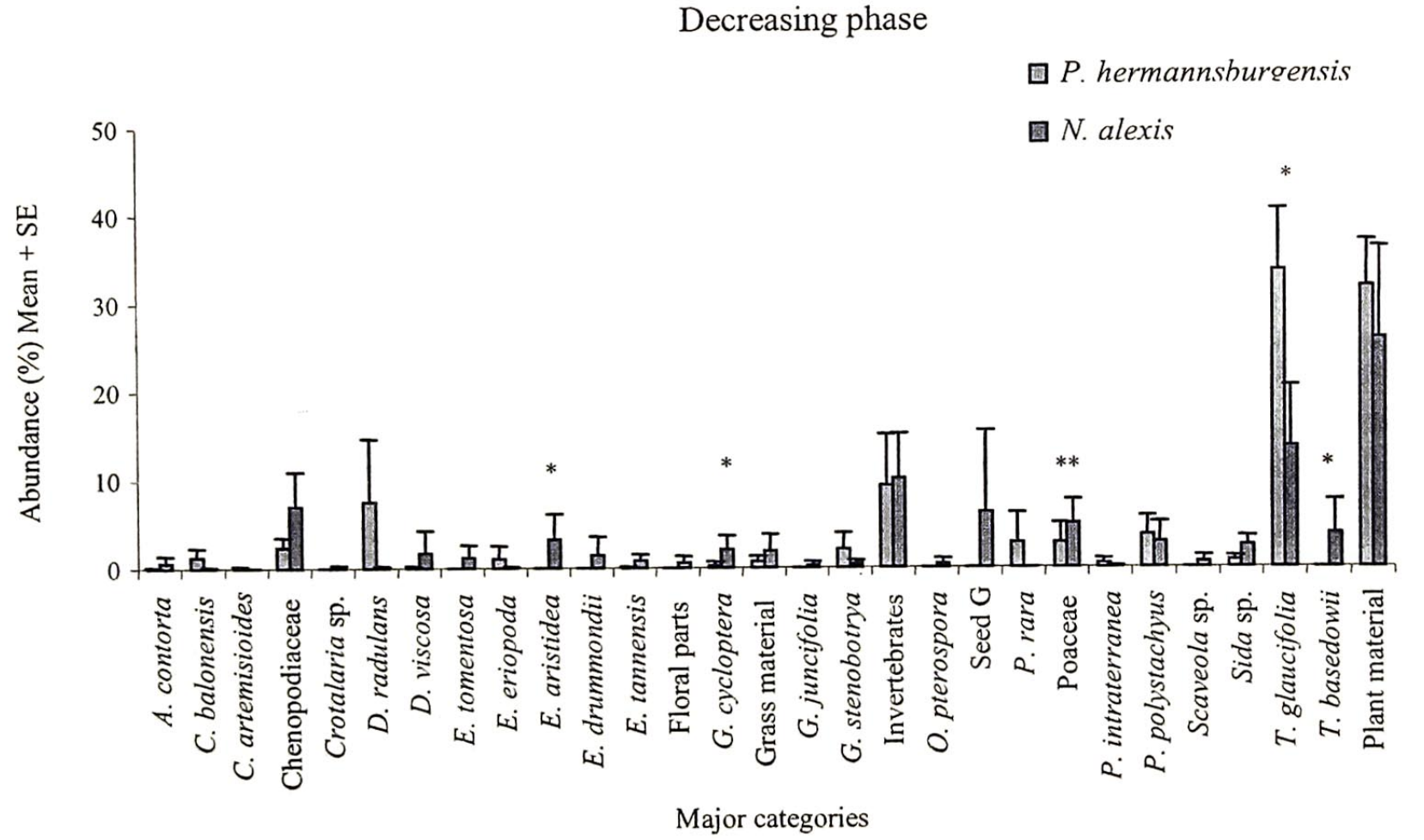

Figure 1. Species- and family-level seeds identified in the diets of the two rodent species during High and Decreasing population phases. The Mann-Whitney test was used to test differences in consumption between species. * $P<0.05$, ** $P<0.01$. Full names of plant species are given in Appendix 3 (Table 1).

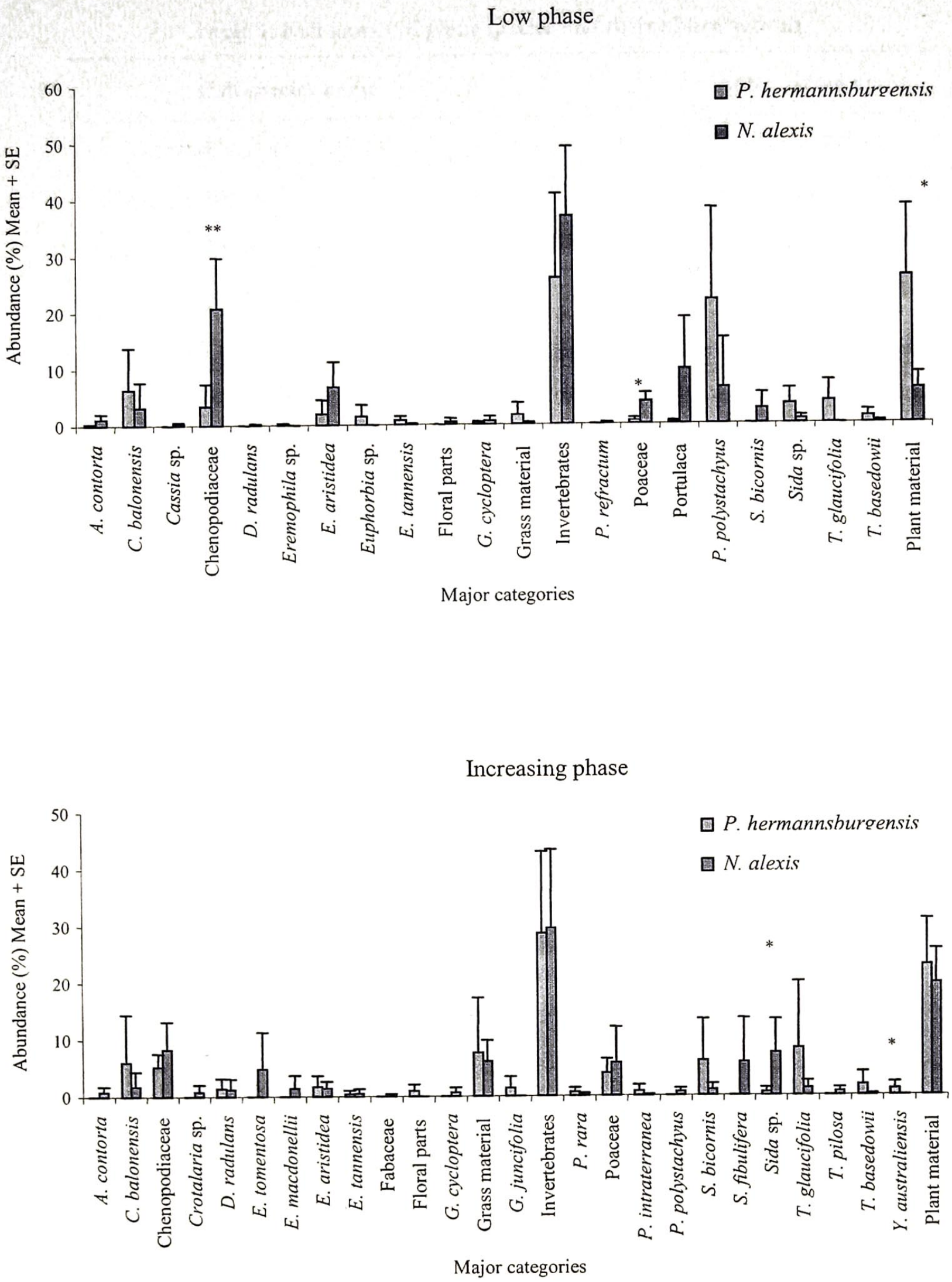

Figure 2. Species- and family-level seeds identified in the diets of the two rodent species during Low and Increasing population phases. The Mann-Whitney test was used to test differences in consumption between species. * $P<0.05$, ** $P<0.01$. Full names of plant species are given in Appendix 3 (Table 1).

Table 1. Full names of plant species and their abbreviations

Full species name	Abbreviated name
Acacia dictyophleba	*A. dictyophleba*
Acacia ligulata	*A. ligulata*
Aristida contorta	*A. contorta*
Atriplex nummilaria	*A. nummilaria*
Calandrinia balonensis	*C. balonensis*
Calotis erinacaea	*C. erinacaea*
Cassia artemisioides	*C. artemisioides*
Crotalaria cunninghamii	*C. cunninghamii*
Crotalaria eremaea	*C. eremaea*
Dactyloctenium radulans	*D. radulans*
Dicrastylis costelloi	*D. costelloi*
Dodonaea viscosa	*D. viscosa*
Enchylaena tomentosa	*E. tomentosa*
Eragrostis eriopoda	*E. eriopoda*
Eremophila longifolia	*E. longifolia*
Eremophyla macdonnellii	*E. macdonnelli*
Eriachne aristidea	*E. aristidea*
Euphorbia drummondii	*E. drummondii*
Euphorbia tannensis var. *eremophila*	*E. tannensis*
Goodenia cycloptera	*G. cycloptera*
Grevillea juncifolia	*G. juncifolia*
Grevillea stenobotrya	*G. stenobotrya*
Helipterum floribundum	*H. floribundum*
Mukia maderaspatana	*M. maderaspatana*
Newcastelia spodotricha	*N. spodiotricha*
Oldenlandia pterospora	*O. pterospora*
Paractaeneum refractum	*P. refractum*
Perotis rara	*P. rara*

Full species name	Abbreviated name
Portulaca intraterranea	*P. intraterranea*
Ptilotus pachyphylla	*P. pachyphylla*
Ptilotus polystachyus	*P. polystachyus*
Salsola kali	*S. kali*
Scaevola parvifolia	*S. parvifolia*
Scaevola spinescens	*S. spinescens*
Sclerolaena bicornis	*S. bicornis*
Sida fibulifera	*S. fibulifera*
Tephrosia rosea	*T. rosea*
Trachymene glaucifolia	*T. glaucifolia.*
Tragus australianus	*T. australianus*
Trianthema pilosa	*T. pilosa*
Tribulus terrestris	*T. terrestris*
Triodia basedowii	*T. basedowii*
Yakirra australiensis	*Y. australiensis*

Table 2. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with average monthly plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons of modified CDMR with capture rates were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain-cover *r***	***P* values**
CDMR(exp) (t=0)	0.459	0.257
CDMR(exp) (t=1)	0.445	0.340
CDMR(exp) (t=2)	0.389	0.730
CDMR(exp) (t=3)	0.455	0.279
CDMR(exp) (t=4)	0.593	0.006
CDMR(exp) (t=5)	0.599	0.005
CDMR(exp) (t=6)	0.602	0.005
CDMR(exp) (t=7)	0.418	0.524
CDMR(exp) (t=8)	0.373	0.830
CDMR(exp) (t=9)	0.103	1.000
CDMR(exp) (t=10)	0.278	1.000
CDMR(exp) (t=11)	0.330	0.976
CDMR(exp) (t=12)	0.292	0.999

Table 3. Correlation coefficients for capture rates of *N. alexis* with average monthly plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***N. alexis* -cover *r***	***P* values**
t=0	0.578	0.010
t=1	-0.152	1.000
t=2	0.563	0.223
t=3	0.816	0.033
t=4	0.235	1.000
t=5	0.603	0.524
t=6	0.110	1.000
t=7	0.781	0.012
t=8	0.582	0.400
t=9	0.431	1.000
t=10	0.599	0.635
t=11	0.467	0.983
t=12	0.619	0.108

Table 4. Correlation coefficients for capture rates of *P. hermannsburgensis* with average monthly plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***P. hermannsburgensis* -cover *r***	***P* values**
t=0	0.574	0.012
t=1	0.650	0.941
t=2	0.598	0.108
t=3	0.712	0.323
t=4	-0.036	1.000
t=5	0.662	0.221
t=6	0.170	1.000
t=7	0.682	0.153
t=8	0.411	0.998
t=9	0.258	1.000
t=10	0.638	0.414
t=11	0.473	0.978
t=12	0.296	1.000

Table 5. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with species diversity of plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain- cover species diversity *r***	***P* values**
CDMR(exp) (t=0)	0.387	0.747
CDMR(exp) (t=1)	0.558	0.020
CDMR(exp) (t=2)	0.440	0.372
CDMR(exp) (t=3)	0.355	0.914
CDMR(exp) (t=4)	0.299	0.998
CDMR(exp) (t=5)	0.085	1.000
CDMR(exp) (t=6)	0.058	1.000
CDMR(exp) (t=7)	0.046	1.000
CDMR(exp) (t=8)	0.121	1.000
CDMR(exp) (t=9)	0.025	1.000
CDMR(exp) (t=10)	0.010	1.000
CDMR(exp) (t=11)	-0.075	1.000
CDMR(exp) (t=12)	-0.086	1.000

Table 6. Correlation coefficients for capture rates of *N. alexis* with species diversity of plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***N. alexis* - cover species diversity *r***	***P* values**
t=0	0.143	1.000
t=1	-0.388	1.000
t=2	0.608	0.086
t=3	-0.369	1.000
t=4	0.012	1.000
t=5	0.793	0.008
t=6	-0.053	1.000
t=7	-0.144	1.000
t=8	0.067	1.000
t=9	0.428	1.000
t=10	0.535	0.916
t=11	0.160	1.000
t=12	0.310	1.000

Table 7. Correlation coefficients for capture rates of *P. hermannsburgensis* with species diversity of plant cover with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***P. hermannsburgensis* - cover species diversity *r***	***P* values**
t=0	0.267	1.000
t=1	0.034	1.000
t=2	0.346	1.000
t=3	-0.303	1.000
t=4	-0.071	1.000
t=5	0.735	0.045
t=6	-0.176	1.000
t=7	-0.307	1.000
t=8	0.097	1.000
t=9	0.141	1.000
t=10	0.434	1.000
t=11	0.257	1.000
t=12	0.231	1.000

Table 8. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with the monthly seed crop index derived from plant surveys with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain-seed index *r***	***P* values**
CDMR(exp) (t=0)	0.584	0.009
CDMR(exp) (t=1)	0.632	0.001
CDMR(exp) (t=2)	0.635	0.001
CDMR(exp) (t=3)	0.256	1.000
CDMR(exp) (t=4)	0.224	1.000
CDMR(exp) (t=5)	0.151	1.000
CDMR(exp) (t=6)	0.158	1.000
CDMR(exp) (t=7)	-0.020	1.000
CDMR(exp) (t=8)	-0.043	1.000
CDMR(exp) (t=9)	-0.154	1.000
CDMR(exp) (t=10)	-0.152	1.000
CDMR(exp) (t=11)	-0.135	1.000
CDMR(exp) (t=12)	-0.140	1.000

Table 9. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with the monthly flower crop index derived from plant surveys with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain-flower index *r***	***P* values**
CDMR(exp) (t=0)	0.462	0.244
CDMR(exp) (t=1)	0.534	0.041
CDMR(exp) (t=2)	0.555	0.022
CDMR(exp) (t=3)	0.205	1.000
CDMR(exp) (t=4)	0.121	1.000
CDMR(exp) (t=5)	0.082	1.000
CDMR(exp) (t=6)	0.029	1.000
CDMR(exp) (t=7)	0.046	1.000
CDMR(exp) (t=8)	0.072	1.000
CDMR(exp) (t=9)	0.067	1.000
CDMR(exp) (t=10)	0.193	1.000
CDMR(exp) (t=11)	0.188	1.000
CDMR(exp) (t=12)	0.145	1.000

Table 10. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with species diversity of the monthly seed abundance derived from plant surveys with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain-seed species diversity *r***	***P* values**
CDMR(exp) (t=0)	0.563	0.017
CDMR(exp) (t=1)	0.711	0.000
CDMR(exp) (t=2)	0.606	0.004
CDMR(exp) (t=3)	0.402	0.640
CDMR(exp) (t=4)	0.357	0.905
CDMR(exp) (t=5)	0.288	0.999
CDMR(exp) (t=6)	0.251	1.000
CDMR(exp) (t=7)	0.102	1.000
CDMR(exp) (t=8)	0.153	1.000
CDMR(exp) (t=9)	0.086	1.000
CDMR(exp) (t=10)	0.128	1.000
CDMR(exp) (t=11)	0.011	1.000
CDMR(exp) (t=12)	-0.016	1.000

Table 11. Correlation coefficients for modified cumulative monthly rainfall residual (CDMR(exp)) with the species diversity of the monthly flower abundance derivate from plant survey with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	**Rain-flower species diversity *r***	***P* values**
CDMR(exp) (t=0)	0.607	0.004
CDMR(exp) (t=1)	0.702	0.000
CDMR(exp) (t=2)	0.589	0.007
CDMR(exp) (t=3)	0.322	0.986
CDMR(exp) (t=4)	0.270	1.000
CDMR(exp) (t=5)	0.198	1.000
CDMR(exp) (t=6)	0.154	1.000
CDMR(exp) (t=7)	0.020	1.000
CDMR(exp) (t=8)	0.069	1.000
CDMR(exp) (t=9)	0.061	1.000
CDMR(exp) (t=10)	0.169	1.000
CDMR(exp) (t=11)	0.076	1.000
CDMR(exp) (t=12)	0.081	1.000

Table 12. Correlation coefficients for capture rates of *P. hermannsburgensis* with the monthly seed crop index, with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***P. hermannsburgensis* - seed index *r***	***P* values**
t=0	0.137	1.000
t=1	0.685	0.842
t=2	0.208	1.000
t=3	0.823	0.027
t=4	-0.115	1.000
t=5	0.055	1.000
t=6	-0.123	1.000
t=7	-0.023	1.000
t=8	0.278	1.000
t=9	0.002	1.000
t=10	0.147	1.000
t=11	0.136	1.000
t=12	0.026	1.000

Table 13. Correlation coefficients for capture rates of *P. hermannsburgensis* with the monthly flower crop index, with time lags. Lags from 0-12 months (t=0 to t=12) are shown. *P* values for multiple comparisons were adjusted using the Dunn-Sidak correction (Sokal and Rohlf 1995). Data from Ethabuka site, March 1990 – December 2001.

Time lags	***P. hermannsburgensis* - flower index *r***	***P* values**
t=0	0.131	1.000
t=1	0.718	0.693
t=2	0.471	0.751
t=3	0.684	0.471
t=4	-0.033	1.000
t=5	0.223	1.000
t=6	0.144	1.000
t=7	-0.030	1.000
t=8	0.630	0.182
t=9	0.787	0.026
t=10	0.017	1.000
t=11	0.385	1.000
t=12	0.198	1.000

Appendix 16

Table 14. Morphological and compositional characteristics of several seed species. E indicates the seed species for which only the kernel was analysed without husks and seed coat. SD, standard deviation, N%, Nitrogen (%), LLD (Largest Linear Dimension), LLD H (Largest Linear Dimension of the Husk), LLD E (Largest Linear Dimension of the Embryo/Endosperm), LLD % E/H, ratio of Embryo/Endosperm to husk of the largest linear dimension of the entire seed, m H, mass of the husk of the entire air-dry seed, m E, mass of the Embryo/Endosperm of the entire air-dry seed, m % E/H, ratio of Embryo/Endosperm to husk of the entire air-dry seed mass, *N* .h.t., *N. alexis* handling time, *P* .h.t., *P. hermannsburgensis* handling time. N/A, handling time not recorded. For abbreviations see also text.

SPECIES NAME	Ash (g)	SD	Energy kJ/g	SD	Water Content (g)	SD	Dry Matter (g)	SD	Protein %	N%	SD	Fat (g)	Carbohydrates (g)	Dietary Fibre (g)	Toxicity	C (g)	H (g)	N (g)	Na (mg)	K (mg)	Mg (mg)	Ca (mg)
Abutilon otocarpum					0.08											0.48	0.07	0.04				
Acacia dictyophleba E	0.01	0.00	22.03	0.62	0.07	0.00	0.93	0.00	36.23	5.80	0.01					0.46	0.07	0.04				
Acacia dictyophleba	0.03		13.68		0.07				23.70			0.07	0.58	0.44					0.60	9.54	2.07	1.53
Acacia dictyophleba			15.19		0.09				23.60			0.07	0.56						0.80	6.41		0.99
Acacia georginae E	0.01	0.00	22.02	0.11	0.07	0.00	0.93	0.00	39.12	6.26	0.04					0.44	0.07	0.05				
Acacia ligulata																						
Acacia ligulata	0.05		14.80		0.04				24.00			0.09	0.58	0.35					0.42	7.62	1.73	1.94
Acacia longifolia	0.04		16.79		0.06				16.30			0.10	0.64						1.22	7.30	2.14	4.39
Acacia melleodora					0.10																	
Aristida contorta E	0.01	0.00	19.67	0.37	0.08	0.00	0.92	0.00	32.64	5.22	0.03											
Atalaya hemiglauca	0.04	0.00	18.89	1.09	0.01	0.00	0.99	0.00	16.84	2.69	0.20					0.44	0.06	0.03				
Calandrinia balonensis																						
Calandrinia balonensis	0.07		17.69		0.06				14.70			0.17	0.55						0.23	0.86		0.86
Calandrinia balonensis	0.07		18.22		0.05				14.60			0.17	0.55						0.23	0.86		0.86
Calotis erinacea																						
Cassia artemisioides E	0.01	0.00	22.83	1.07	0.04	0.00	0.96	0.00	47.68	7.63	0.16											
Cassia artemisioides	0.04	0.00	19.41	0.65	0.07	0.00	0.93	0.00	18.32	2.93	0.38					0.40	0.06	0.03				
Cassia nemophila	0.03	0.00	18.98	0.64	0.06	0.00	0.94	0.00	18.37	2.94	0.25											
Cassia oligophylla	0.03	0.00	17.30	0.44	0.10	0.09			16.31	2.61	0.07											
Cassia pleurocarpa E	0.01	0.00	22.60	0.72	0.05	0.00	0.95	0.00	42.76	6.84	0.03											
Cassia pleurocarpa	0.03	0.00	19.98	0.35	0.08	0.02	0.92	0.02	20.12	3.22	0.85											
Cenchrus ciliaris																0.38	0.05	0.01				
Cleome viscosa	0.01	0.00	23.98	0.50	0.05	0.00	0.95	0.00	15.46	2.47	0.44											
Commercial mixed seeds	0.03	0.00	18.05	0.36	0.10	0.00	0.90	0.00	11.01	1.76	0.23											
Crotalaria cunninghamii E	0.03	0.00	19.19	0.75	0.34	0.01	0.66	0.01	27.37	4.38	4.28				poss alkaloids							
Crotalaria eremaea	0.04	0.00	22.09	1.60	0.10	0.01	0.90	0.01	29.62	4.74	6.89				poss alkaloids	0.44	0.06	0.05				
Dactyloctenium radulans E	0.01	0.00	17.73	0.54	0.08	0.00	0.92	0.00	20.65	3.30	0.06				poss nitrates	0.39	0.05	0.01				
Dicrastylis costelloi	0.08	0.01	21.44	0.48	0.05	0.01	0.95	0.01	3.65	0.58	0.20					0.49	0.06	0.00				
Dodonaea viscosa E	0.01	0.00	25.29	0.15	0.04	0.00	0.96	0.00	32.21	5.15	0.03											
Dodonaea viscosa	0.03	0.00	21.58	0.51	0.07	0.00	0.93	0.00	19.24	3.08	0.12											
Enneapogon polyphyllus E	0.01	0.00	20.02	0.40	0.07	0.00	0.93	0.00	34.92	5.59	0.04											
Eragrostis eriopoda E	0.01	0.00	18.02	0.53	0.07	0.00	0.93	0.00	15.55	2.49	0.10											
Eragrostis eriopoda	0.02		13.31		0.09				16.20			0.02	0.65	0.09					0.22	1.86	1.56	1.18
Eragrostis eriopoda	0.02		15.05		0.10				15.76			0.01	0.70						0.31	1.60		0.59
Eremophila longifolia																						
Eremophyla macdonnellii E	0.02	0.00	25.30	0.16	0.03	0.00	0.97	0.00	29.22	4.68	0.02											
Eriachne aristidea E	0.01	0.00	18.81	0.19	0.07	0.00	0.93	0.00	20.22	3.23	0.00											
Eucalyptus gamophylla					0.08																	
Eucalyptus gamophylla	0.08		17.76		0.08				25.90			0.20	0.38						0.35	0.81		5.05
Eucalyptus gamophylla	0.08				0.08				26.00			0.20	0.38						0.35	0.91		5.05
Eucalyptus microtheca					0.16																	
Eucalyptus pachyphylla E	0.02	0.00	21.93	1.74	0.05	0.00	0.95	0.00	27.35	4.38	0.16											
Euphorbia drummondii															poss cyanide	0.41	0.05	0.01				
Fimbristylis dichotoma E	0.04	0.01	18.11	1.22	0.05	0.00	0.95	0.00	12.45	1.99	0.01											
Fimbristylis oxystachya	0.20		11.08		0.11				11.00			0.19	0.43						0.45	1.73		0.39
Fimbristylis oxystachya	0.19		17.13		0.05				13.95			0.18	0.43						0.21	2.09		0.55
Goodenia cycloptera	0.02	0.00	24.79	0.16	0.06	0.00	0.94	0.00	16.23	2.60	0.08					0.51	0.07	0.02				
Grevillea juncifolia					0.17																	
Grevillea stenobotrya E	0.06	0.01	29.43	0.94	0.04	0.00	0.96	0.00	31.80	5.09	0.22					0.52	0.07	0.03				
Hibiscus krichauffianus																						
Lepidium rotundum																0.48	0.07	0.05				
millet																0.40	0.06	0.01				
Mix budgerigar	0.04	0.01	18.00	0.38	0.06	0.00	0.94	0.00	11.90	1.90	0.12											
Mix cockatiel	0.03	0.00	19.47	0.21	0.06	0.00	0.94	0.00	14.64	2.34	0.09											
Mix small parrot	0.02	0.00	20.32	0.41	0.06	0.00	0.94	0.00	16.48	2.64	0.12											
Newcastelia entire	0.01	0.00	20.86	0.26	0.06	0.00	0.94	0.00	3.06	0.49	0.07					0.49	0.06	0.00				
Newcastelia husks	0.01	0.00	19.88	0.58	0.06	0.00	0.94	0.00	3.67	0.59	0.01											
Nicotiana megalosiphon	0.03	0.00	25.04	0.41	0.04	0.00	0.96	0.00	23.08	3.69	0.00											
Oldenlandia pterospora E	0.06	0.01	22.52	1.97	0.06	0.00	0.94	0.00	14.34	2.29	0.07											
Othonna gregorii	0.01	0.00	20.83	0.57	0.06	0.00	0.94	0.00	19.05	3.05	0.12											
Paractaeneum refractum E	0.01	0.00	19.37	0.44	0.07	0.00	0.93	0.00	24.54	3.93	0.02					0.42	0.06	0.02				
Portulaca intraterranea																0.47	0.06	0.03				
Portulaca intraterranea	0.02		4.90		0.62				2.00			0.00	0.27	0.05					0.95	4.50	2.00	1.15
Ptilotus latifolius																						
Ptilotus polystachyus E	0.02	0.00	20.07	0.71	0.08	0.00	0.92	0.00	26.59	4.25	0.10											
Scaevola parvifolia																						
Sclerolaena bicornis E	0.01	0.00	19.08	0.37	0.05	0.00	0.95	0.01	27.05	4.33	0.09											
Setaria surgens	0.13	0.01	18.66	1.57	0.06	0.00	0.94	0.00	8.72	1.39	0.39											
Sida fibulifera					0.21											0.43	0.05	0.01				
Sida platycalyx	0.04	0.00	19.51	0.53	0.06	0.00	0.94	0.00	26.68	4.27	0.73											
Stylobasium spathulatum E	0.01	0.00	24.94	0.10	0.04	0.00	0.96	0.00	40.74	6.52	0.08											
Stylobasium spathulatum	0.02		5.15		0.01				12.30			0.03	0.80						3.26	6.13		0.55
Stylobasium spathulatum									44.50			0.28										
sunflower																0.58	0.08	0.04				
Swainsona microphylla	0.05	0.00	19.42	0.37	0.08	0.00	0.92	0.00	37.45	5.99	1.73											
Trachymene glaucifolia E	0.00	0.00	26.13	0.34	0.05	0.00	0.95	0.00	18.40	2.94	0.01											
Trachymene glaucifolia	0.02	0.00	23.03	0.80	0.07	0.00	0.93	0.00	12.40	1.98	0.25				poss unidentified	0.49	0.07	0.02				
Tragus australianus E	0.01	0.00	17.21	0.32	0.07	0.00	0.93	0.00	20.95	3.35	0.02											
Trianthema pilosa E	0.03	0.01	22.23	0.62	0.07	0.00	0.93	0.00	16.92	2.71	0.04											
Trichodesma zeylanicum E	0.01	0.00	27.75	0.30	0.03	0.00	0.97	0.00	27.72	4.43	0.05				poss alkaloids							
Triodia basedowii E	0.02	0.00	18.08	0.13	0.08	0.00	0.92	0.00	21.38	3.42	0.22					0.40	0.07	0.03				
Triumfetta winneckeana																0.49	0.07	0.03				
Yakirra australiensis					0.16																	
Yakirra australiensis	0.08		14.97		0.08				16.60			0.05	0.62						0.21	1.17		0.29
Zygophyllum howittii															poss nitrates	0.41	0.06	0.05				

Fe (mg)	Zn (mg)	Cu (mg)	LLD (mm)	SD	LLD H (mm)	SD	LLD E (mm)	SD	LLD % E/H	Mass (mg)	SD	m H (mg)	SD	m E (mg)	SD	m % E/H	SD	Hardness	SD	*N.* h.t. (s)	SD	*P.* h.t. (s)	SD	Source
			2.28	0.23						1.80	0.45							0.17	0.08					McNaught (1994)
			4.19	0.59						10.37	5.58									21.00		25.00		actual study
.04	0.03	0.02																						Brand Miller *et al*. (1993)
																								Latz (1996)
			8.89	3.69						86.20								0.84	0.11					McNaught (1994), actual study
			11.06	2.93						65.20	19.23							0.08	0.01					McNaught (1994)
.07	0.02	0.01																						Brand Miller *et al*. (1993)
.81	0.03	0.03																						Brand Miller *et al*. (1993)
			5.24	2.10						14.00								0.10	0.02					McNaught (1994)
			9.06	1.04	94.48	6.97	6.48	0.50	6.86	1.58		6.06	0.40	1.78	0.14	29.40	1.52	0.07	0.02	5.80	1.80	11.10	4.80	McNaught (1994), actual study
																				80.00		N/A		actual study
			0.83	0.67						0.10														McNaught (1994)
																								Brand Miller *et al*. (1993)
																								Latz (1996)
			3.57	1.23						2.60								0.13	0.07					McNaught (1994)
																								actual study
			6.10	1.02						20.30	3.13							0.04	0.02					McNaught (1994), actual study
																								actual study
																								actual study
																				33.00		68.00		actual study
			6.10	1.72						27.00								0.04	0.01					McNaught (1994), actual study
																								actual study
			1.13	0.16						0.92	0.21									10.00		7.00		actual study
																								actual study
			5.97	0.76						55.00								0.09	0.02					McNaught (1994), actual study
			4.54	1.47						24.67								0.06	0.02					McNaught (1994), actual study
			1.03	0.06						0.29														actual study
			4.10	0.61						20.30								0.13	0.02	40.00		56.00		McNaught (1994), actual study
																				10.10	6.90	28.70	15.10	actual study
			3.41	0.54	3.21	0.42	2.11	0.23	65.77	17.50		7.95	0.52	3.39	0.34	42.60	1.55	0.09	0.03					McNaught (1994), actual study
			2.64	0.09						3.40								0.29	0.12					McNaught (1994), actual study
			0.88	0.08	1.82	0.19	0.85	0.07	46.54	0.14		0.99	0.14	0.12	0.07	11.99	5.51			3.50	1.90	3.40	1.50	actual study
.31	0.05	0.01																						Brand Miller *et al*. (1993)
																								Latz (1996)
			7.00	0.27						119.70	44.27							0.08	0.03					McNaught (1994)
			11.66	1.77						291.00								0.28	0.09	2.20		2.70		McNaught (1994), actual study
			4.81	0.23	12.18	2.84	1.84	0.24	15.09	2.18		1.80	0.24	0.36	0.16	19.50	6.78	0.43	0.24	4.50	2.10	7.40	3.10	McNaught (1994), actual study
			3.77	1.45						3.01								0.63	0.38					McNaught (1994)
																								Brand Miller *et al*. (1993)
																								Latz (1996)
			1.58	0.19						0.42														McNaught (1994)
			2.68		2.68	0.86	2.68	0.86	100.00	1.63		1.63	0.23	1.27	0.23	77.90	6.36			3.50	2.80	8.50	3.80	actual study
			2.97	0.17						2.11								0.54	0.20					McNaught (1994)
			1.08	0.10						0.21														actual study
																								Brand Miller *et al*. (1993)
																								Latz (1996)
			5.48	0.71	5.63	0.48	4.82	0.37	85.61	1.25		4.74	0.43	3.24	0.07	68.73	5.01	0.27	0.03	21.80	10.80	22.00	10.60	McNaught (1994), actual study
			16.45	2.91						31.00	22.14							0.42	0.28	66.00		114.00		McNaught (1994), actual study
			12.58	1.57	12.38	0.92	7.48	0.38	60.38	23.30		27.67	1.67	17.42	1.62	62.85	2.24	0.58	0.07	24.70	19.50	58.10	15.40	McNaught (1994), actual study
			2.91	0.09						6.40	8.27							0.21	0.14					McNaught (1994)
																								actual study
																								actual study
																								actual study
																								actual study
																								actual study
			6.80	2.01						8.35								0.08	0.01	58.00		70.00		McNaught (1994), actual study
																								actual study
																				1.40		1.60		actual study
			1.24		1.24	0.30	1.24	0.30	100.00	0.22		0.22	0.02	0.22	0.02	100.00	0.00			1.70	0.80	3.80	2.30	actual study
			22.60	3.32						4.11	1.07									21.00		19.00		actual study
			4.66	0.40	24.15	3.26	2.84	0.40	11.75	4.18		3.88	0.33	0.65	0.24	16.42	5.20	0.41	0.09	3.60	1.00	9.00	2.10	McNaught (1994), actual study
																				0.85-		1.50		actual study
0.24	0.01	0.00																						Brand Miller *et al*. (1993)
			1.97	0.08						0.90	0.45							0.56	0.31					McNaught (1994)
			10.90	2.25	13.96	0.68	1.41	0.34	10.13	3.40	0.67	4.28	0.64	0.79	0.23	18.21	2.51	0.49	0.25	10.20	4.40	15.30	7.80	McNaught (1994), actual study
			7.67	1.30						3.33								0.13	0.03					McNaught (1994)
			5.37	1.15						59.50								0.21	0.06					McNaught (1994), actual study
																								actual study
			7.08	1.59						3.40								0.78	0.16					actual study
																				25.00		28.00		actual study
			7.14	1.13						168.00								0.03	0.01	N/A		N/A		McNaught (1994), actual study
																								Brand Miller *et al*. (1993)
																								Latz (1996)
																								actual study
			2.30	0.17						2.40	0.45							0.10	0.01					McNaught (1994), actual study
																				19.00		33.00		actual study
			5.76	1.08						1.36								0.13	0.01					McNaught (1994), actual study
			3.84		3.84	0.47	0.98	0.26	25.44	0.87		0.81	0.16	0.06	0.05	6.95	4.80			3.20	1.30	4.40	0.70	actual study
			6.94	0.83						5.77	2.16													actual study
			3.69	1.14	4.68	0.40	3.26	0.33	69.62	7.80	2.68	13.33	0.11	6.62	0.20	49.68	1.68	0.63	0.15	8.70	1.90	23.40	10.10	McNaught (1994), actual study
			2.45	0.74	6.52	0.59	1.10	0.19	16.87	1.69		1.18	0.06	0.10	0.08	8.27	6.59	0.11	0.01	10.10	9.70	8.40	5.90	McNaught (1994), actual study
																				N/A		N/A		actual study
			1.88	0.15						1.18										1.80		3.00		McNaught (1994), actual study
																								Latz (1996)
			6.44	0.30						9.60	0.89							0.14	0.04					McNaught (1994), actual study

Table 15. Models of multiple regression on seeds consumed by *P. hermannsburgensis* in seven experiments. The model in each experiment with the lowest AIC is in bold and represents the best fit. R^2 and *P* values for each model are presented in separate columns. AIC (Akaike Information Criterion) is used to compare different models. See Chapter 6 for explanation of variables used in models.

Exp #	Model	R^2	AIC	*P*
1	**Carbon-Hardness**	**0.976**	**-11.369**	**0.024**
1	Ash-Hydrogen	0.957	-8.594	0.043
2	**Water-*N*.h.t.**	**1**	**-45.597**	**0.012**
2	LLD-*N*.h.t.	1	-45.597	0.013
3	**Ash-Water-Protein**	**1**	**-34.586**	**0.01**
3	Ash-Energy-Protein	1	-29.093	0.026
3	Ash-Protein	0.973	-9.710	0.027
4	**Ash-Energy-Water**	**1**	**-27.654**	**0.026**
4	DryMatter-Protein-LLD	0.999	-25.627	0.033
4	Ash-Energy-DryMatter	0.999	-23.073	0.044
4	Dry Matter- Water	0.974	-9.352	0.026
4	Dry Matter-Mass	0.973	-9.288	0.027
4	Dry Matter-LLD	0.953	-6.517	0.047
5	**Protein-LLD-Mass**	**1**	**-31.120**	**0.023**
5	Dry Matter-LLD-Mass	0.999	-25.627	0.036
6	**Water-DryMatter-Protein-LLD**	**1**	**-42.197**	**0.01**
6	Ash-Water-Protein-LLD	1	-42.197	0.014
6	Ash-DryMatter-Protein-LLD	1	-35.605	0.024
6	Energy-DryMatter-Protein-LLD	1	-31.447	0.032
6	Water-Protein-LLD	0.992	-16.216	0.012

Table 16. Models of multiple regression on seeds consumed by *N. alexis* in seven experiments. The model in each experiment with the lowest AIC is in bold and represents the best fit. R^2 and *P* values for each model are presented in separate columns. AIC (Akaike Information Criterion) is used to compare different models. See Chapter 6 for explanation of variables used in models.

Exp #	Model	R^2	AIC	*P*
1	**Hydrogen-Mass-Hardness**	**1**	**-57.612**	**0.004**
1	Ash-Carbon-Hydrogen	1	-34.586	0.012
1	Water-Hydrogen-Nitrogen	1	-34.586	0.018
1	Water-Protein-Hydrogen	1	-31.120	0.024
1	Protein-Carbon-Hardness	0.999	-25.627	0.039
1	Protein-Hardness	0.992	-17.127	0.008
1	Nitrogen-Hardness	0.991	-16.641	0.009
1	Water-Hydrogen	0.991	-16.459	0.009
1	Hydrogen-Hardness	0.971	-10.820	0.029
1	Ash-Hydrogen	0.968	-10.377	0.032
1	Carbon-Hardness	0.959	-9.100	0.041
2	**Hardness** (calculated on only three seed species)	**1**	**-47.597**	**0.003**
3	**Ash-Energy-Water**	**1**	**-57.612**	**0.009**
3	Energy-Water-LLD	0.999	-24.856	0.038
3	Energy-Water-Protein	0.999	-23.073	0.044
3	Ash-Protein	0.964	-8.202	0.036
4	**Ash-Energy-Water**	**1**	**-57.612**	**0.008**
4	Ash-Energy-DryMatter	1	-57.612	0.009
4	Dry Matter-Protein-Weight	1	-34.586	0.013
4	Dry Matter-LLD-Weight	0.999	-29.093	0.031
4	Dry Matter-Mass	0.991	-16.927	0.009
4	Dry Matter-LLD	0.955	-8.959	0.045
5	No model significant	N/A	N/A	N/A
6	Water-Protein-LLD	0.957	-6.526	0.063

Table 17. The best model, as shown in Appendix 16 (Table 14), for each experiment for *P. hermannsburgensis*. R^2, F, degrees of freedom and P values are reported below the model for each experiment. Rank = mean preference rank for dietary items.

Exp 1	Rank = - 17.572 + 22.044 **Carbon** - 4.722 **Hardness** R^2=0.976 $F_{2,2}$=39.859 P=0.024
Exp 2	Rank = 3.144 - 17.911 **Water** + 3.180 ***N*.h.t.** R^2=1 $F_{2,1}$=3629.138 P=0.012
Exp 3	Rank = - 12.067 + 20.733 **Ash** + 1.585 **Water** + 22.821 **Protein** R^2=1 $F_{3,1}$=5043.317 P=0.010
Exp 4	Rank = - 2.987 + 10.246 **Ash** + 35.192 **Energy** - 163.932 **Water** R^2=1 $F_{3,1}$=779.370 P=0.026
Exp 5	Rank = 25.309 - 45.153 **Protein** - 3.365 **LLD** + 3.439 **Mass** R^2=1 $F_{3,1}$=1058.192 P=0.023
Exp 6	Rank = - 4.375 + 34.960 **Water** - 5.462 **Dry Matter** + 13.326 **Protein** - 3.837 **LLD** R^2=1 $F_{4,1}$=5665.060 P=0.010

Table 18. The best model, as shown in Appendix 17 (Table 15), for each experiment for *N. alexis*. R^2, F, degrees of freedom and P values are reported below the model for each experiment. Note that even though the model of experiment 6 is not significant, it has been presented anyway, because P value approaches the significance and R^2 is high. Note that in Exp 2 **Hardness** was measured only for three of the four seed species. However, it has been presented here as the only significant result obtained in Exp 2 for *N. alexis*. Rank = mean preference rank for dietary items.

Exp 1	Rank = 13.466 - 45.083 **Hydrogen** - 0.386 **Mass** - 1.789 **Hardness** R^2=1 $F_{3,1}$=38879.377 P=0.004
Exp 2	Rank = 0.392 - 2.520 **Hardness** (Regression calculated just on three seed species) R^2=1 $F_{1,1}$=34452.638 P=0.003
Exp 3	Rank = - 44.573 - 10.061 **Ash** + 33.861 **Energy** + 12.531 **Water** R^2=1 $F_{3,1}$=7323.748 P=0.009
Exp 4	Rank = -1.963 + 11.058 **Ash** + 27.300 **Energy** - 127.906 **Water** R^2=1 $F_{3,1}$=7957.078 P=0.008
Exp 5	No model significant
Exp 6	Rank = - 14.190 + 40.886 **Water** + 14.391 **Protein** - 2.994 **LLD** R^2=0.957 $F_{3,2}$=14.939 P=0.063

Table 19. Results of the breeding experiment carried out on *P. hermannsburgensis* maintained on different diets: Standard and Spinifex. Mean mass of litter (g) is shown at one month. N/A means no data are available. "Alive" means that the litter survived until the end of the study. When pups were wholly or partially eaten the mass and the sex are not reported. This is the reason for the lack of standard deviation (SD) in some cases.

Diet + Pair	Days elapsed to birth	Size of litter	Litter survival (days)	Mean mass of litter ± Stdev	Age of litter at first weight (days)	Sex ratio	Weaning time (days)
Standard 1	N/A	0	N/A	N/A	N/A	N/A	N/A
Standard 2	137	1	14 killed and eaten	N/A	N/A	N/A	N/A
Standard 3	N/A	0	N/A	N/A	N/A	N/A	N/A
Standard 4	43	3	alive	3.60 ± 0.42	30	0 M:3 F	29
Standard 5	378	2	alive	7.36 ± 0.91	30	1M:1 F	24
Standard 6	N/A	0	N/A	N/A	N/A	N/A	N/A
Spinifex 1	128	4	rescued after 30 days, one killed and eaten	3.68 ± 0.33	30	3+? M: ? F	34
Spinifex 2	N/A	0	N/A	N/A	N/A	N/A	N/A
Spinifex 3	132	2	one killed at 15 days, one alive	6.68	37	2 M: 0 F	30
Spinifex 4	42	3	28 killed and two half-eaten	4.91	28	2 M: 1 F	N/A
Spinifex 5	175	3	19 mother stopped feeding them	2.58 ± 0.18	19	3 M: 0 F	N/A
Spinifex 6	N/A	0	N/A	N/A	N/A	N/A	N/A