Dietary shifts in vertebrates: factors affecting seed selection in desert rodents

Sandy inland mouse (*Pseudomys hermannsburgensis*)

Photo: Stephanie Joyce Shui-Lin Yip

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Statement of Originality

This is to certify that to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted, either in part or in whole, for any degree or other purposes at The University of Sydney or any other institution.

I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

Signature

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Abstract

The underlying premise for this study is based on foraging theory, which predicts that small vertebrates forage in ways that allow them to maximize their net rate of energy gain or to minimize their risk of starvation. The sandy inland mouse (*Pseudomys hermannsburgensis*), an Australian desert rodent, is the principal focus of study, in part because of its abundance and tractability for hypothesis testing, and in part because it provides an opportunity to compare its patterns of foraging activity with those of more extensively-studied rodents in arid North America. My experiments on foraging and seed selection focused on diet shifts when animals are under the risk of predation, diet choice in relation to seed characteristics and the background seed base (the 'familiarity effect'), and the foraging characteristics of animals when seed accessibility was manipulated by burying seeds at different depths in the soil profile and with different amounts of moisture.

To ensure that the experimental focus on seeds was appropriate, I first confirmed that seeds are an important component of the diet by making direct observations of foraging animals and analyzing the stomach contents of *P. hermannsburgensis.* The results confirmed the species to be omnivorous, with seed forming a major component of the diet. Experiments using giving-up density trials and cafeteria trials with different seed species showed animals to be risk-averse and less active in open compared with sheltered areas. Under low predation risk animals selected preferred seed types, whereas under high risk they were less choosy and quickly took whatever seeds they encountered, thus reducing their potential exposure to predators. Further experiments showed that *P. hermannsburgensis* uses olfaction to detect seeds buried at depths up to 5 cm, but prefer seeds that are available on the soil surface; moist seeds do not affect seed detection or consumption. The mice were shown to prefer familiar compared with rare seeds in further experiments, although other factors such as seed quality are also important. Experimental exclusion of rodents from plots showed finally that seed predation reduces seed species diversity and abundance, but these effects became clear only after a major rainfall event that triggered an eruption in rodent numbers and predation impact.

My research constitutes the first detailed study of the diet and foraging behaviour of an Australian desert rodent. It uncovers a range of novel strategies that allow *P. hermannsburgensis* to persist in its variable desert environment, and contrasts these strategies with those used by rodents in other world deserts.

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Chapter 1. General Introduction

The primary objective of this thesis is to explore the diet, foraging habits and factors that influence foraging in desert rodents, focussing in particular on the diet and foraging habits of one common and widespread Australian desert species, the sandy inland mouse (*Pseudomys hermannsburgensis*). Working in the Simpson Desert, central Australia, I hope to gain insight into general foraging theory and expand the current knowledge of foraging habits in rodents which may be used in future autecological studies and assist in informing conservation decisions.

Foraging theory

"Choose the option that maximises the objective, subject to constraints." (Stephens *et al.*, 2007).

Foraging behaviour in animals has long fascinated observers of the natural world. In *Historia Animalium* in 350 BC, for example, Aristotle described the feeding habits of predatory birds and the selection of preferred foods by several different species of mammals (Thompson, 2007). Further observations on a range of species were recorded in *Naturalis Historia* ca. AD 77 by Pliny the Elder (Healy, 1991). More-recent observations of foraging behaviour have highlighted the highly diverse means by which animals acquire food (e.g., Darwin, 1859), but have also attempted to explain why some food types are taken and others are rejected. Some of this early thinking focused on the benefits and constraints that animals face when foraging, such as would-be prey running away or fighting back (Darwin, 1859), decision-making by foragers about whether to eat now or postpone foraging until times when better-quality prey might be found (Lorenz, 1949), and how animals might judge the quality of different food types when several are available (Leyhausen, 1956). Then, in important papers in 1959, Holling initiated the development of a theoretical framework that could be used to interpret and explain some of the many disparate observations of foraging that had been made previously. This development recognised that animals expend time and effort in searching for food, and then in identifying and handling it, and that food types consumed by a forager should vary with prey density (Holling, 1959a,b).

Following Holling's work, two publications appeared that are often viewed as the foundations of modern foraging theory. These appeared as consecutive papers in 1966 in the *American Naturalist*; the first was by Robert MacArthur and Eric Pianka ('On optimal use of a patchy environment') and the second by John Merritt Emlen ('The role of time and energy in food preference'). Both papers suggested that the processes of prey encounter and prey selection were shaped by evolution so that animals would maximize their net energy gain per unit time while feeding (Schoener, 1987). The integration of time and energy as foraging currencies provides an important underpinning for much current understanding of animal foraging behaviour (Pyke *et al*., 1977; Pyke, 1984; Stephens *et al*., 2007).

Foraging models, in particular optimality models, are generally comprised of the following components that are not always mutually independent: 1) decision assumptions, 2) currency assumptions and 3) constraint assumptions (Stephens and Krebs, 1986). Decisions are choice variables or options that are under the control of the organism, and these can be static (one choice will not impact another choice) or dynamic (one choice could potentially impact a future decision). In early optimal foraging models four decisions were considered important: what patch type to visit/occupy, how much time to spend in a patch, which type of food to eat while in each patch type, and finally which foraging path to use to access each patch (Pyke *et al.*, 1977). More-recent foraging models focus largely on what prey items to consume and when to leave any given patch for another, especially if the models are being subjected to empirical testing (Stephens and Krebs, 1986; Stephens *et al.*, 2007).

Currency is used to compare different outcomes from a decision variable, and is an objective function or goal (Stephens and Krebs, 1986; Stephens *et al.*, 2007). There are many different types of currency; positive outcomes are commonly modelled using energy or nutrients in food, or time; negative currencies include the chance of starving or being eaten (Pyke *et al*., 1977). Currency is linked further to choice principles such as maximisation, minimisation and stability (Stephens and Krebs, 1986) which need to be balanced by foragers. Consider, for example, an animal that seeks to maximise energy intake per unit time. It could choose to use the least amount of time to gain a certain amount of food and therefore minimise the currency of time, or it could attempt to gain more energy in a fixed amount of time and thereby maximise the currency of food/energy.

Constraints limit both decisions and currency, with constraint assumptions being mainly that foragers cannot exploit a patch or food item while simultaneously looking for new ones, that food items are met one at a time and at a constant rate (sequential Poisson encounters), and that external factors such as predators, competitors and weather may curtail foraging at particular times or places. Foragers are also expected to behave within other rules of the model, which may specify other constraints due to genetics, physiology, neurology, morphology, as well as the basic laws of chemistry and physics (Stephens and Krebs, 1986; and Stephens *et al.*, 2007).

The term 'optimal foraging theory' was the original rubric used to describe foraging models, but the optimality aspect is now often downplayed. Some authors criticise the premise of optimal foraging theory, stating that it is unreasonable to view organisms as 'optimal' and that foragers must make so many decisions that optimality is unrealistic both in theory and in practice (Pierce and Ollason, 1987). However, 'optimality' may be used in foraging theory not to describe the organism itself or its system, but rather to describe the method or the general rule-set that an organism uses to feed (Stephens *et al.*, 2007).

Currently, much of the focus of foraging theory is the idea that the behaviour of foraging animals is affected by their prey and by external constraints. Thus, animals forage in a manner that is most advantageous to them, such as by maximising net energy intake per unit time and expending as little energy as possible in this process, and avoiding becoming prey themselves while foraging (Krivan, 1996). The main components that are important in developing and testing foraging theory are diet (which prey to select), patch choice, when to leave a patch, movement between patches and central place foraging (e.g., where animals return to a base after each foraging bout); all these components are affected by stochasticity and random variables in most environments that make approaches to 'optimality' very difficult (Pyke, 1984).

One of the most common predictions of foraging theory is that organisms should seek to achieve maximum net rate of energy or mass intake (E_n/T) while foraging (the 'energy maximizing model'). To achieve this, a forager must: select food of higher preference rank as measured by the ratio of food value and handling time, regardless of abundance; be able to perceive and consume more preferable food than is available; and that food items must be accepted or rejected, there should be no partial consumption (Pyke *et al.*, 1977; Lacher *et al.*, 1982).

Krebs *et al.* (1977) demonstrated the energy maximizing model using great tits (*Parus major*) under experimental conditions with food offered on a moving belt, and showed that when the encounter rate with both profitable and unprofitable prey types was low, the birds were non-selective, but at a higher encounter rate with profitable prey, the birds selectively ignored the less profitable type and did so irrespective of the encounter rate with them. Lacher *et al.* (1982) also provided some evidence to support the energy maximizing model, using a folivore, the rock cavy (*Kerodon rupestris*: Caviidae) with access to 10 different species of leaves. However, this experiment also found that preference changed over time, and there was some partial consumption of less preferred food even though the higher ranked food was abundant. In other work, Indian crested porcupines (*Hystrix indica*) were shown to discriminate between two types of resources and selected habitats with denser cover and therefore lower foraging costs (Brown and Alkon, 1990), while fox squirrels (*Sciurus niger*) exhibited similar behaviour as more food was taken from safer areas near bushes rather than from riskier open areas (Brown *et al.*, 1992).

Resource acquisition is necessary for growth, reproduction and overall fitness; however, it is not the only factor: obtaining food needs to be balanced with the imperative to survive, especially if other, larger predators are present (Stephens *et al.*, 2007). There is often a trade-off between feeding and danger, as often better-quality foraging sites are in more dangerous sites (Stephens *et al.*, 2007). The fear of predation affects many aspects of foraging and may reduce the time that animals will attempt to feed in exposed situations. For example, desert gerbils decrease foraging activity on nights when the moon is full as there is therefore a higher chance of being seen by predators (Hughes *et al.*, 1994). Fear of predation also affects habitat choice, as animals may need to choose between habitats that differ in productivity or in provision of shelter. Kotler (1984), for example, showed that small quadrupedal mammals such as the little pocket mouse (*Perognathus longimembri*) and deer mouse (*Peromyscus maniculatu*) choose to spend more time in areas with bushes that provide protection than in open areas with more food. Fear of meeting a predator can also restrict and influence animal movements, with some vulnerable animals limiting the distance they travel for foraging. To reduce the chances of being killed by predators, some foragers increase detection behaviours such as scanning and vigilance; which increases survival from predation, but decrease the rate of food consumption as time and focus is spent on scanning (Stephens *et al.*, 2007). The presence of relatively safe and risky areas within foragers' ranges has led to the recent concept of the 'landscape of fear', in which mobile animals must trade-off the benefits of exploiting food-rich parts of the landscape against the risks that are posed by encountering predators while foraging there (Laundré *et al.*, 2009, 2017; Bleicher, 2017).

Foraging models

Many early models of foraging were verbal or graphical (e.g., MacArthur and Pianka, 1966) and, while useful as heuristic tools, the predictions that they could yield about the behaviour of foragers were relatively general. More explicit predictions about foraging can be made by writing simple equations. These have the advantage that the components of foraging can be specified with precision, but empirical tests of models may be difficult if input parameters are hard to measure and if the test environment is subject to much stochastic variation. Some examples are shown in the sections below.

Modelling foraging under risk of predation

M(u) = mortality

$$\mathrm{M(u)} = \mathrm{ku^z}$$

k = mortality constant

z = mortality exponent

u = measure of foraging effort

Foraging for a fixed time

$$W(u) = S(u)V(u) = [\exp(-ku^z)][Ku]$$

W = fitness

u = measure of foraging effort

S = survival

V = future reproductive values

k = mortality constant (or can be considered danger)

z = mortality exponent

K = foraging effort into future offspring

optimal foraging effort u*

$$u* = \frac{1}{\sqrt[z]{kz}}$$

only if

$$u* \geq R$$

u*= differentiated foraging effort

R = some required effort

The above equations show the trade-offs between foraging effort, mortality risk and the effects of net foraging success on the ability of animals to reproduce and their consequent fitness. As foraging effort increases so does fitness, but this will decrease as constant k increases as the higher danger this implies reduces the time that animals can forage (Stephens *et al*., 2007). For this equation unlimited food is assumed to be available, and therefore a forager must consider the danger of being eaten by a predator and must limit its time spent foraging to reduce its chances of dying from predation.

Gathering resources with no time limit

$$W(u) = \exp[-M(u)T(u)]\, V]$$

W = fitness

u = measure of foraging effort

M = Mortality

T = Time

V = future reproductive values

$$T(u) = \frac{K}{u} - R$$

K = foraging effort into future offspring

R = required

$$u *= \frac{zR}{z-1}$$

z = mortality exponent

This equation defines the gain of a fixed amount of resources from foraging within a potentially unlimited time. If the food requirement, R, is large then it is best to forage at a maximum rate of u = 1, as the mortality constant k is not present and only z is included; the exact level of danger is not important for animals in this environment with limited food and unlimited time, and animals should simply maximise their foraging to maximise fitness (Stephens *et al.*, 2007). In this equation food is a limited resource and, therefore, foraging outweighs the danger of being eaten by a predator: the animal must focus more time and energy foraging as the risk of dying from starvation is higher than the risk of death by predation.

In this thesis I aim to test predictions that can be derived from these models, doing so in the field using a native species of Australian rodent, the sandy inland mouse (*Pseudomys hermannsburgensis*). This species has a wide distribution that covers most of arid Australia, using microhabitats that provide dense cover in sandy deserts, acacia- and chenopod-dominated shrublands, alluvial flats, gibber plains and occasionally rock outcrops (Finlayson, 1941; Gibson, 1986; Dickman, 1993). In sand dune desert foraging occurs mainly on the sides of dunes and in the dune swales (Predavec, 1994, 1997). The species is nocturnal and quadrupedal, with an average mass of 12 g (Watts and Aslin, 1981; Breed and Ford, 2007).

Although considered previously to be granivorous (e.g., Watts and Aslin, 1981), *P. hermannsburgensis* has been shown more recently to be omnivorous and to include varying amounts of invertebrate and plant material in its diet, depending on season (Murray and Dickman, 1994a,b; Murray *et al.*, 1999). Nonetheless, seed still comprises a major part of the diet of *P. hermannsburgensis*, and for this reason it is a good case study species whose foraging behaviour can be compared with the better-studied and largely granivorous rodents of South America, and especially North America (e.g., Kelt, 2011; Arregoitia and D'Elía, 2021). As a common and still widespread species, study of *P. hermannsburgensis* may also help to illuminate factors that have helped it to persist when many other of Australia's arid-dwelling species have declined or become extinct in recent times.

Decline of mammals in Australia

Although mammals have been declining rapidly around the world (Woinarski *et al.*, 2015), Australia has the highest extinction rate of mammals in the last 200 years with over fifty percent of the world's mammal extinctions coming from Australia (Short and Smith, 1994; Smith and Quin, 1996). In Australia, arid and semi-arid regions have experienced higher rates of mammal extinction than other, higher rainfall environments; over the last 200 years desert regions have seen at least 21 mammal extinctions of the 34 extinctions documented in total for the mainland, offshore islands and island territories (Woinarski *et al.*, 2011; Spencer *et al.*, 2014; Woinarski and Fisher, 2023). Native rodents have been greatly affected, with fourteen mostly desert-dwelling species (21% of rodents present in 1788) having become extinct and many more species in decline (Smith and Quin, 1996; Woinarski *et al.*, 2011).

The extinction of most mammals, particularly of rodents, has been linked to many factors associated with the arrival of European settlers to Australia including habitat loss and transformation, introduction of livestock, the introduction of rabbits (*Oryctolagus cuniculus*) and feral predators such as the feral cat (*Felis catus*) and the European red fox (*Vulpes vulpes*) (Smith and Quin, 1996; Woinarski *et al.*, 2011).

Aims, scope and contribution of the thesis

There has been limited research on the diets of Australian rodents, and the foraging habits of most species remain relatively unexplored (Watts and Aslin, 1981; Murray and Dickman, 1994a,b; Murray *et al.*, 1999; Breed and Ford, 2007). Although it is a common species, this paucity of research extends to *P. hermannsburgensis*, especially with respect to the factors that influence its foraging behaviour. In this thesis, I hope to build on the foundations of foraging theory as outlined above and extend our understanding into aspects of diet quality rather than simply the net rate of energy gain that can be made by foragers. I will show that energetic gain and risk of predation are not the sole drivers of foraging decisions by prey organisms, and that other factors can also impact foraging decisions and influence the quality of forager diets, especially the variety of different types of food that are eaten.

In addition to being an instructive case study species for foraging theory, there are several further reasons why *P. hermannsburgensis* was selected for study. Although it is common and not facing immediate extinction, *P. hermannsburgensis* is regionally vulnerable in New South Wales and southern parts of Western Australia (Dickman, 1993). Most conservation efforts are geared towards priority species that are at the greatest risk of extinction, especially those that may become extinct in the near future; this is a logical strategy as once lost it is (currently) impossible to reverse an extinction. However, common species should not be forgotten (Breed and Ford, 2007; Gaston and Fuller, 2008). Firstly, common species are often more important to the structure of ecological communities than rare species owing to their relatively greater biomass and contribution to ecological processes and interactions; and secondly historical records show that many previously common species underwent significant declines that were unremarked until numbers had crashed due to the perception that they remained abundant, some examples of previously common species include the passenger pigeon (*Ectopistes migratorius*) and the saiga (*Saiga tatarica*) (Gaston and Fuller, 2008). *P.hermannsburgensis* is an important prey species for various native predators such as small and mid-sized dasyurids, birds of prey, goannas and snakes; it is also important to feral predators such as feral cats and red foxes (Spencer *et al*., 2014, 2017). Major declines of *P. hermannsburgensis* populations could lead to prey switching by these predators, putting more pressure on other prey species (Mahon, 1999). Thus, while it is clearly pre-emptive to create a conservation strategy for *P. hermannsburgensis*, it is useful to have basic knowledge of its ecology, such as habitat and dietary requirements, factors that influence its behaviour and the impact of feral animals on the species, as management action can be taken more quickly if there is a population decline or if the species does become more vulnerable to extinction due to existential factors such as climate change or threats from feral species. Aspects of the biology of *P. hermannsburgensis* are outlined further in Chapter 2.

Understanding the foraging habits of *P. hermannsburgensis* can be useful also in reflecting the foraging habits of other rodents, especially species that may be endangered and difficult to observe directly, thus facilitating more effective conservation decisions that relate to their diets and foraging behaviour (Murray and Dickman, 1994b; Jackson *et al*., 2023). It has been proposed that availability of food is the main limiting factor for populations of *P. hermannsburgensis* (Breed, 1990; Beh, 2011) and, while supplementary feeding may not reverse population declines, it is able to slow the overall rate of decline (Predavec, 2000). In more recent research, Dickman *et al*. (2010) suggested that predation may have a greater impact on populations of *P. hermannsburgensis* than reduced food resources, as populations declined faster than their food resources. By investigating the foods encountered and eaten by *P. hermannsburgensis*, its response to predation risk and its effects on its food base, it is hoped that this thesis makes contributions both to foraging theory and to empirical understanding of a common but poorly understood native rodent species.

Hypotheses and predictions

The broad objective of this thesis is to study the diet of the sandy inland mouse (*Pseudomys hermannsburgensis*), an Australian desert rodent, and to determine the factors that influence its foraging behaviour. To further this broad objective, several specific aims and hypotheses have been developed from the review of foraging theory and the biology of *P. hermannsburgensis* presented above. Each of these aims forms a data-chapter in this thesis:

Hypothesis 1

The diet of *P. hermannsburgensis* will be dominated by seed material over different seasons and years, with smaller contributions made by invertebrates and green plant parts.

Hypothesis 2

Based on the findings that the diet of the *P. hermannsburgensis* is primarily based on seed from the previous hypothesis, the effect of risk of predation can be observed using seed cafeteria trials. Using the assumption of foraging theory that animals will spend less time foraging while under high risk of predation, I predict that *P. hermannsburgensis* under low risk of predation will have the time to select preferred seed species, whereas animals under high risk of predation will have less time to be selective and will consume the range of seed species that they encounter.

Hypothesis 3

According to foraging theory animals will use minmal time and effort to gain maximum rewards when foraging. Thus I predict that *P. hermannsburgensis* will take seeds that minimise time and effort to collect and are easy to detect (moist seeds on the soil surface) in preference to seeds that are costly to collect and difficult to find (dry seeds that are buried in the soil).

Hypothesis 4

As animals forage to maximise survival they will forage on foods that provide the most energetic or nutritional benefit. Thus I predict that *P. hermannsburgensis* will prefer seeds they are familiar with (seeds that are found commonly in seed bank in the area) rather than consume seeds that are rare or foreign, as common seed would be identified and consumed more quickly by the animal and therefore reducing time spent foraging.

Hypothesis 5

The previous hypotheses indicated that seeds play an important role in *P. hermannsburgensis* diet. As *P. hermannsburgensis* is one of the most common rodent species in arid areas, I predict that soil seedbanks will differ in areas with and without these foraging rodents.

Structure of the thesis

This thesis has been written to facilitate publication. Thus the primary data chapters, 3 to 7, are formatted as research papers for different target journals and differ slightly in their format and spelling (English vs US). Because the chapters are intended to be mostly publication-ready there is inevitably some repetition, especially with sections that are common to all data chapters such as the study area and background on the target species. In addition, because of the intended journal submissions each chapter has its own list of references that were used in the chapter; some references are therefore cited repeatedly between chapters. However, to economise, all references cited in Chapters 1 and 2 are combined and presented at the end of Chapter 2.

Chapter 2. Study site and study species

Study site

Research was conducted in the Simpson Desert, central Australia. Around 73% of this 170,000 km^2 desert region is comprised of dune fields, with smaller areas consisting of clay pans, rocky outcrops and gibber flats (Greenville *et al.*, 2013). Work was carried out primarily on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E) (Dickman *et al.*, 2010). This arid study site, on Wangkamadla traditional lands, is now managed by Bush Heritage Australia and has been the focus of work by the Desert Ecology Research Group (University of Sydney) for over 30 years.

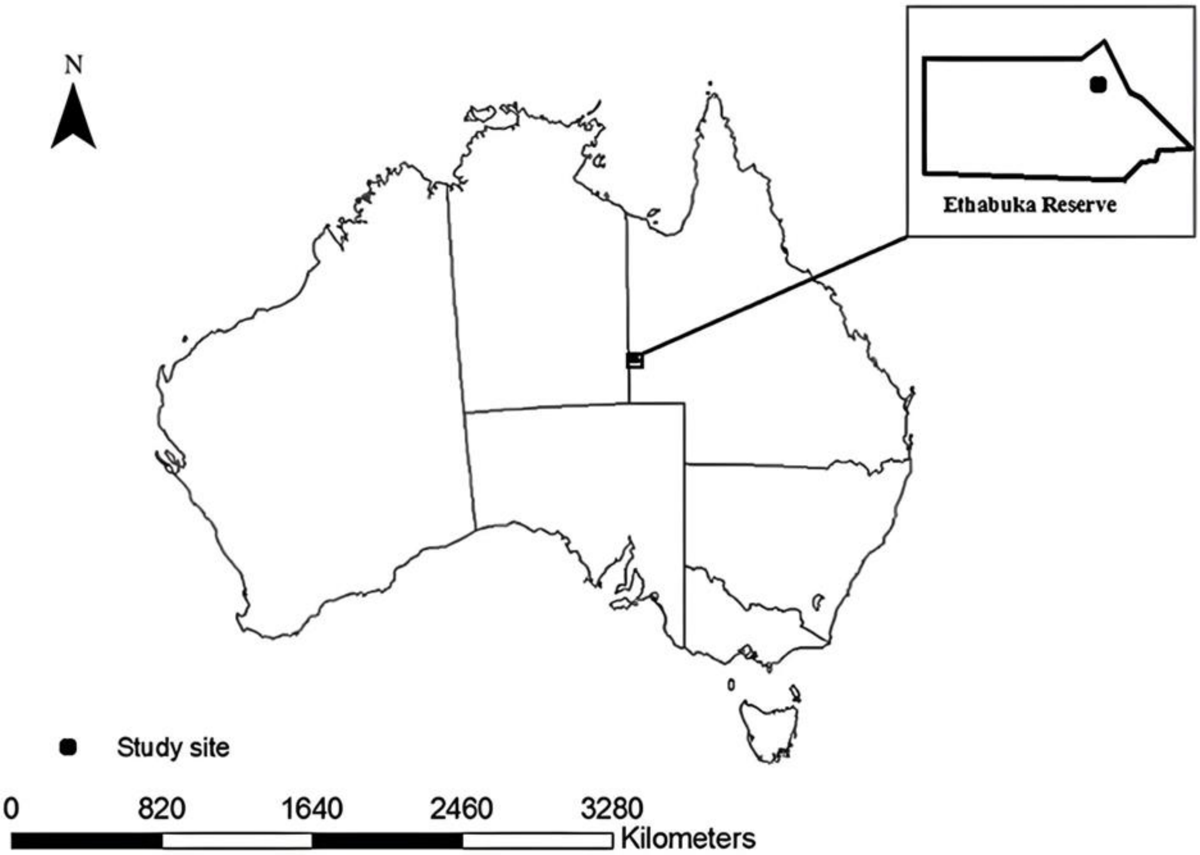

Fig 1. Location of study area on Ethabuka Reserve in western Queensland, Australia. Source: Greenville and Dickman (2009)

Ethabuka Reserve is dominated by long, parallel sand dunes that lie 0.6–1.0 km apart and rise to about 8–10 m high (Dickman *et al.*, 2011). The dominant vegetation of the research site is needle-leaved hard spinifex (*Triodia basedowii*), which is mainly confined to the floors of the dune valleys and slopes to just below the dune crests. On low-lying clay soils in the dune valleys there are patches of gidgee (*Acacia georginae*) woodland that cover < 0.5 ha to > 10 ha and comprise 7–16% of the study region. Under the open gidgee canopy where spinifex is not present, chenopod shrubs such as *Enchylaena tomentosa, Salsola kali, Atriplex* spp., and *Sclerolaena* spp. occur (Wardle *et al.*, 2015). Other shrubs such as *Acacia ligulata, A. dictyophleba, Eucalyptus pachyphylla, E. gamophylla, Grevillea stenobotrya,* and *G. juncifolia* occur sporadically in the dune fields and, depending on rainfall, annual grasses, forbs, and herbs may grow abundantly, but persist during long dry periods in seed banks (Dickman *et al.*, 2010, 2011).

The Simpson Desert is classified as a hot desert, with daily maximum temperatures in summer reaching 46–49°C, and winter temperatures dropping down to −6°C (Purdie, 1984; Dickman *et al.*, 2011). The climate is dominated by the El Niño/Southern Oscillation and is highly irregular (Letnic and Dickman, 2006). Ethabuka Reserve lies along a north-south rainfall gradient and most rain falls during the austral summer between October and March; the average long-term rainfall is 199 mm/year (Dickman *et al.*, 2010, 2011). Wildfires occur at the study site, with a mean minimum return interval of 26 years (Greenville *et al.*, 2009), as heavy summer rains cause excess vegetation growth and after 1-2 years the vegetation dries out and becomes fuel to allow fires to spread rapidly across the landscape (Verhoeven *et al.*, 2020). There are two distinct and disparate periods in the desert. The ‘bust’ phase refers to times when it is dry and unproductive, while the ‘boom’ phase describes short periods of high productivity resulting from heavy rainfall or flooding. These periods are usually linked to El Niño/Southern Oscillation (ENSO) cycles, with the boom phase occurring during the La Nińa phase (Dickman *et al.*, 1999, 2010; Letnic and Dickman, 2010; Greenville *et al.*, 2017).

The two dominant species of rodents in the study site are the sandy inland mouse (*Pseudomys hermannsburgensis,* ~12 g) and spinifex hopping-mouse (*Notomys alexis,* ∼30 g). Other species such as the house mouse *Mus musculus* are very scarce in the area, and the long-haired rat *Rattus villosissimus* is rarely seen unless there is an extreme rainfall event with rainfall exceeding the 95th percentile; in such 'boom' conditions, populations of the latter species can erupt to plague proportions (Dickman *et al.*, 2011; Greenville *et al.*, 2013). The main potential competitor of *P. hermannsburgensis* for resources is *Notomys alexis* with a high overlap of types of food eaten, but there are some differences in seed preferences that likely reduce direct competition. While both species are often found in the same areas they prefer different microhabitats with *N. alexis* foraging in open areas and *P. hermannsburgensis* being more commonly found in or around spinifex grass hummocks (Murray and Dickman, 1994a).

The main large mammalian predators in the Simpson Desert are feral cats (*Felis catus*), European red foxes (*Vulpes vulpes*), and dingoes (*Canis dingo/familiaris*) and all three are found on Ethabuka Reserve (Spencer *et al*., 2014).

Study species: sandy inland mouse (*Pseudomys hermannsburgensis*)

This thesis focussed on the foraging habits of the sandy inland mouse (*Pseudomys hermannsburgensis*); as noted in Chapter 1, this species is found across Australia in semi-arid and arid areas, often in hummock grasslands, but also in other habitats such as mallee shrublands and acacia woodlands (Watts and Aslin, 1981; Predavec, 1994; Breed and Ford, 2007). The mice have been recorded to burrow in large intersexual groups, with females mating polyandrously over short periods; males perforce appear to engage in sperm competition leading to litters that are usually sired by more than one male (Breed and Ford, 2007; Firman, 2014). Evidence that the species mates polyandrously was provided by Firman *et al*. (2013) with paternity analysis of litters indicating mixed paternity based on allele counting, and the main author also observed in a laboratory setting that female *P. hermannsburgensis* will readily and actively initiate copulations with more than two males (Firman 2014). Reproduction is aseasonal, with animals breeding from 3 months of age, and gestation is 30-34 days (Watts and Aslin, 1981; Breed, 1990; Breed and Ford, 2007).

Diet

Initially it was assumed *P. hermannsburgensis* was a granivore, with Watts (1974: 112) stating ‘it is known that the desert rodents *Pseudomys* and *Notomys* eat mainly seed with some green plant material’. This statement was based on the earliest quantitative data on the species in the arid zone (Watts, 1970), which was obtained in what the author classed as a ‘good season’. In 1983 Watts and Morton, using scats of *P. hermannsburgensis*, found that seed contributed up to three quarters of the diet, but the species also consumed insects and at times insects contributed substantially to the diet; this research was conducted when the conditions were considered ‘average’ or ‘arid’ and when individuals were sparse. Research conducted in western Queensland by Murray and Dickman (1994a) using a much larger sample size and stomachs from animals collected in different seasons during periods of both high and low abundance determined the trophic status of *P. hermannsburgensis* to be omnivorous, not granivorous as previously assumed. However, seeds still made an important contribution to the diet of *P. hermannsburgensis* during summer and especially in winter. Further research using scats of *P. hermannsburgensis* from the Tanami Desert, Northern Territory, confirmed that the mice are omnivorous, with the species eating a diverse range of foods and invertebrates and seeds both being important and contributing to the diet in all seasons. The importance of these diet components shifted seasonally, with insects being more significant during autumn and seeds during summer (Murray *et al*., 1999).

Physiological adaptations

Pseudomys hermannsburgensis has numerous physiological adaptations to allow it to survive and thrive in semi-arid and arid environments. Animals are able to efficiently conserve water by producing highly concentrated urine, faeces with low water content, by being nocturnal, and living in communal burrows with high humidity; lactating females consume the faeces and urine from young to mitigate some water loss from lactation (Baverstock and Elhay, 1979; MacMillen and Hinds, 1983; Murray *et al.*, 1995). Indeed, MacMillen *et al*. (1972) showed that animals could persist indefinitely on a diet of air-dried seed with no access to free water. To survive extreme temperature fluctuations *P. hermannsburgensis* uses facultative hypothermia/torpor and benefits from living communally to maintain warmth and reduce energy loss at low temperatures (Tomlinson *et al.*, 2007; Tomlinson and Withers, 2009).

Pseudomys hermannsburgensis has a relatively low basal metabolic rate, a common trait of desert rodents that gives animals the advantage of being able to conserve energy and water and increase their longevity. This trait is therefore selectively advantageous in the variable arid environment, allowing the rodents to survive times of ‘bust’ and then breed when conditions improve (MacMillen, 1983; Predavec, 1997), even though *P. hermannsburgensis* is still able to breed during prolonged dry periods (Breed, 1990; Breed *et al.*, 2017). Another advantage of living in group burrows is that this aids rapid reproduction when conditions improve as it ensures access to mates and/or generates synchronised breeding. This can facilitate polyandry and presumably also increase the fitness of offspring by increasing the genetic diversity of litters (Firman, 2014).

Predators

The predators of *P. hermannsburgensis* include the dasyurid marsupials *Dasycercus cristicauda* and *D. blythi* (mulgaras), birds of prey, goannas, snakes, cats, foxes and, to a lesser extent, the dingo (Mahon, 1999). Rodents are the most important vertebrate group in the diet of brush-tailed mulgara *D. blythi* during winter and spring, with this mulgara then having a mostly insect-based diet in autumn (Chen *et al.*, 1998); it has been observed in laboratory settings that mulgaras have a preference for mice over other prey items (Sorenson, 1970). *P. hermannsburgensis* also occurs frequently in the diet of the Australian sand goanna *Varanus gouldii* (Dickman *et al.*, 2022). Dickman *et al.* (2022) also found that *P. hermannsburgensis* would avoid foraging in areas with *V. gouldii* odour and that *V. gouldii* was attracted to areas with *P. hermannsburgensis* odour and actively dug at burrows that had been experimentally laced with the mouse odour. The letter-winged kite *Elanus scriptus,* barn owl *Tyto alba* and eastern barn owl *Tyto delicatula* are nocturnal birds that frequently prey upon *P. hermannsburgensis*. Although barn owls often consume other rodent species such as the house mouse *Mus musculus* or hopping-mice *Notomys* spp. in greater numbers than *P. hermannsburgensis*, especially during rodent eruptions, the owls often switch to higher consumption of *P. hermannsburgensis* when populations of the other rodents such as the long-haired rat (*Rattus villossimus*) and house mouse (*Mus musculus*) crash (Kutt *et al.*, 2020). During the crash, or bust period, *P. hermannsburgensis* can become more significant in the diet of the barn owl, and may also feature prominently in the diet of the eastern barn owl (Morton *et al.*, 1977; Morton and Martin, 1979; Heywood and Pavey, 2002; Pavey *et al.*, 2008a,b; Kutt *et al.*, 2020).

The feral cat *Felis catus* and the European red fox *Vulpes vulpes* are both introduced predators to Australia, the feral cat being first recorded in the central deserts in 1880s and the red fox in the early 1900s (Dickman, 1996; Abbott, 2002; Yip *et al.,* 2014; Vernes *et al.*, 2021). Both the feral cat and the red fox have been linked to the decline and extinction of a range of native wildlife species since their introduction to Australia over 150 years ago (Dickman, 1996; Spencer *et al*., 2014; Fleming *et al*., 2022). The European red fox is an opportunistic predator that includes a high proportion of mammals in its diet, with a preference in arid areas for small to medium-sized mammals (Dickman, 1996; Spencer *et al*., 2014). The feral cat is usually considered a generalist predator that hunts a range of small vertebrates. However, it exhibits some preference for, and specialization on, small mammals, especially those weighing less than 40 g, which includes *P. hermannsburgensis*. Feral cats often specialise on small rodents, using finely-honed hunting skills and an ability to stalk prey and use cover to their advantage (Dickman, 1996, 2009; Spencer *et al*., 2014; Yip *et al.,* 2014; Vernes *et al*., 2021).

The dingo (*Canis dingo/familiaris*) is the largest native mammalian predator in Australia. While it will hunt *P. hermannsburgensis*, the mice play a relatively small role in dingo diet; dingoes prefer medium to large-sized mammals such as rabbits, cattle and kangaroos (Paltridge, 2002; Spencer *et al*., 2014, 2017; Vernes *et al*., 2021).

Population fluctuations

Rodent populations in arid environments often fluctuate dramatically between years, with very low densities during long term droughts, or ‘busts’, to transient but high numbers during ‘booms’ when densities can reach >25/ha; exceptionally >100/ha (Finlayson, 1941, 1961; Dickman *et al.,* 2010). The booms are driven by heavy rainfalls that cause strong resource pulsing with increases in invertebrate populations and a surge in germination and growth of ephemeral, annual and perennial plant species and the recruitment of perennials such as trees and shrubs (Letnic and Dickman, 2010). After heavy rainfall rodents will often breed shortly after and the subsequent young are able to flourish with the abundance of food from the rain (Breed, 1990; Breed and Ford, 2007; Breed *et al*., 2017); populations increase rapidly within

3-10 months after a rainfall event and the high population usually persists for 1-2 years before declining (Predavec, 1994; Dickman *et al.*, 2010; Letnic and Dickman, 2010).

The main cause of decline of rodent populations post-rain is the rapid loss of food and shelter resources. Food declines as it is consumed by the large rodent populations, and subsequent drought and lack of water mean that invertebrates and plant productivity fade. Supplemental provision of food has been found in *P. hermannsburgensis* to slow the overall rate of population decline, but not to reverse it (Predavec, 2000; Beh, 2011; Prevedello *et al.*, 2013). Wildfire may also play a role in the decline of rodent populations as, after a fire occurs, food and shelter are significantly reduced over large areas (Letnic *et al.*, 2013).

Another factor suggested to expedite the rapid decline of rodent populations after a boom, and which is often exacerbated by wildfire, is predation, particularly from feral cats and red foxes (Dickman *et al.*, 2010; Letnic *et al.*, 2013). While cats can persist in low numbers in arid areas during bust periods and during a boom will increase in numbers through breeding and increased survival of young, red foxes often disappear from arid areas during busts and then migrate back in during boom periods due to the dramatic increase in prey (Letnic and Dickman, 2006). The result is heavy *per capita* predation on small mammals such as *P. hermannsburgensis*, which can then be driven to very low population levels at the of the next bust period (Letnic and Dickman, 2006; Spencer *et al.*, 2014, 2017; Yip *et al.*, 2015; Greenville *et al.*, 2017).

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Chapter 3. Foraging and seed selection in rodents: the diet of the sandy inland mouse *Pseudomys hermannsburgensis*

Abstract

The diet of the sandy inland mouse (*Pseudomys hermannsburgensis*) was studied in the Simpson Desert, south-western Queensland, Australia, using direct observations of animals foraging in the field and analysis of stomach contents of preserved specimens. Direct observations showed that animals forage mostly on the ground surface and eat seeds from a wide range of plant species, as well as smaller numbers of invertebrates and occasional green plant material. Stomach contents from specimens collected over different seasons and years were analyzed to score the presence or absence of these three major food classes (seeds, plant material, invertebrates). The results indicated no difference in diets between the sexes or the four seasons that were examined. The results also confirm that seed is a major component of the diet of *P. hermannsburgensis*, with 92% of stomachs containing seed. The results also support the classification of the species as omnivorous rather than granivorous, with 70% of stomachs containing invertebrates and over half the specimens analyzed containing both seeds and invertebrates. Invertebrates appear to play a more significant role in the diet of *P. hermannsburgensis* during bust periods; there is an increased incidence of this food type in the diet during bust compared to boom periods, with this dietary shift probably reflecting a scarcity of seeds during the bust periods.

Introduction

Compared to desert rodent species in many parts of the world (North America, South America, Middle East, and South Africa), where dietary studies have often been a focus, there is a lack of detailed information relating to the foods selected and eaten by native Australian rodents. In North America, for example, heteromyid rodents have been much-studied, and the primarily granivorous diets and seed-caching behaviours of many species predicted that all desert rodents could be expected to be granivorous (e.g., Mares, 1975, 1980, 1993). In South America, seeds comprise a large proportion of the diets of many species, notably in arid regions, but invertebrates, fungi and green plant material often form additional components of the diet (Campos *et al*., 2001; Prevedello *et al.,* 2017). In Africa, the consumption of seeds and green plants by rodents has resulted in extensive studies in many cropping areas due to the destructive impacts of species such as multimammate rats (*Mastomys* spp.) (Fiedler, 1988; Granjon *et al.*, 2005); however, desert rodents have also been subject to considerable study, with some authors suggesting that granivory is the norm for rodents of small and medium body mass (Kerley & Whitford, 1994). Relatively fewer rodent species occur in Australia than in other continental regions, but quantitative analyses of diet are still limited and distributed patchily among extant taxa (e.g., Cockburn, 1981; Murray *et al.*, 1999).

The sandy inland mouse (*Pseudomys hermannsburgensis*) provides a good example of a native species for which only limited dietary information is available, with most of the detailed research conducted more than twenty years ago (e.g., Murray & Dickman, 1994a, 1994b; Murray *et al.*, 1999; Predavec, 1994; Predavec, 1997). The relative paucity of relevant information is surprising in that *P. hermannsburgensis* has the largest extant distribution of any native rodent and is often the numerically dominant member of desert mammal assemblages (Watts & Aslin, 1981).

The chapter focuses on the foraging and diet of *P. hermannsburgensis* in sand dune habitats in central Australia. In addition to furthering our understanding of the diet of this species, this initial study was intended to form the basis of subsequent research in this thesis. For example, if seeds were confirmed to form the major dietary component of *P. hermannsburgensis*, then subsequent foraging experiments based on seeds would be most appropriate; if invertebrates were more prominent than expected, then further exploration of how animals hunt for these prey would be appropriate.

Foraging usually occurs in or near microhabitats that provide dense cover which, in sand dune habitats, is mainly amongst hummock grasses on the sides of dunes and in the dune swales (Predavec, 1994, 1997). This species is nocturnal and quadrupedal with an average mass of 12 g (Predavec, 1994). In early work it was believed that the species was almost solely granivorous, this classification being based on the diets of ecologically similar species that had been studied in deserts in other parts of the world (Mares, 1993; Kerley & Whitford, 1994), and on the examination of small samples of 4–6 *P. hermannsburgensis* stomachs (Watts, 1970; Morton, 1979; Watts & Morton, 1983). Murray and Dickman (1994a) and Murray *et al*. (1999) later suggested that at least 10 individuals are required to sample dietary diversity reliably. More detailed analyses of the diet of *P. hermannsburgensis* with larger sample sizes revealed the species to be omnivorous and to have a variable diet containing invertebrates, seeds and plant material (Murray & Dickman, 1994a,b; Murray *et al*., 1999). While *P. hermannsburgensis* can be best classified as an omnivore, seeds are still a major component of its diet, with the proportion and relative importance of seeds differing over time and potentially over different seasons (Murray & Dickman, 1994a) and at different times in the boom and bust cycles that characterise the desert environment (Ricci, 2003).

This study used two complementary methods to determine the diet of *P. hermannsburgensis*: direct observations in the field, and stomach analysis. Direct observations can provide detailed insight into the foraging mode of the species being observed as well as document food items that are selected or rejected. However, as *P. hermannsburgensis* is nocturnal and cryptic, making observations can be time-consuming and fraught with challenges to ensure that normal foraging is not disturbed. By contrast, faecal or stomach analysis provides a snapshot look at the foods consumed during one bout of foraging, but can be challenging because food items are often finely comminuted and partially digested, making identification difficult. In this study stomach analysis was carried out, rather than faecal analysis, for a number of reasons. Firstly, stomachs from various seasons were readily available as these had been collected during previous long-term research projects by the Desert Ecology Lab at the University of Sydney; and secondly, there are some advantages in using stomach contents versus faeces, or scats, such as the food items being less digested. This makes food items easier to identify and reduces the time spent on analysis (Ward, 1970); also, scats often return less reliable results than stomach contents, especially for seed-eating rodents, due to the greater degree of digestion of material that has passed the length of the digestive tract (Brand, 1978). Based on previous observations, I expected seed to be the predominant food type in the diet of *P. hermannsburgensis*, but also that the relative importance of seeds and other food types would vary with calendar season and with boom and bust conditions.

Methods

Study site

Research was conducted on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E). The landscape has long parallel sand dunes up to 8 m high and 0.5-1 km apart with hard claypans forming between the dunes (Murray & Dickman, 1994a). The major vegetation is spinifex *Triodia basedowii* with ephemeral herbs and perennial shrubs dominating the dune crests such as *Crotalaria* spp. and *Grevillea* spp.; in the swales there are stands of trees such as mulga *Acacia aneura*, and gidgee *Acacia georginae* (Wardle *et al*., 2015).

The average rainfall can vary greatly, oscillating between periods that are either dry and unproductive (‘bust’ periods) or wet/flooded due to extreme rainfall events that cause brief pulses of high productivity (‘boom’ periods). Most rainfall occurs in summer with occasional heavy rainfall locally and regionally at other times (Greenville & Dickman, 2005; Dickman *et al*., 2010). Over an average of 94 years 199 mm/year of rain was measured at Marion Downs (a station located 120 km from Ethabuka), but rainfall can differ significantly between years. For example, an average 214.2 mm fell in 1999, and well above average 496.6 mm of rain fell in 2000 (Greenville & Dickman, 2005; Dickman *et al*., 2010). Temperature varies widely depending on season, with average daily temperature exceeding 40°C in summer, and during winter average minimum temperatures often fall below 5°C (Greenville & Dickman, 2005). Following Murray and Dickman (1994a), summer was taken to cover the months of December to February, autumn from March to May, winter from June to August, and spring September to November. Significant rainfall events (>90th percentile) occurred over the spring and summers of 1990-91, 2000-01, 2010-11 and 2015-16, resulting in population eruptions of *P. hermannsburgensis* and many other consumer species such as the long-haired rat (*Rattus villossimus*) and budgerigar (*Melopsittacus undulatus*) (Dickman *et al*., 2014; Bureau of Meteorology, 2022).

Direct observations of foraging

Pseudomys hermannsburgensis was observed in the field on 24 visits to the study site between November 2010 and June 2022. Most of these animals had been captured in pitfall traps set in the sand dune environment on the previous night, using trapping protocols that have been described in detail in Dickman *et al*. (1999, 2010, 2014). The animals were removed from the traps and placed individually in perspex holding cages (24 × 16 × 20 cm high) that had been provisioned with a 1-cm substrate of sand, dry leaf litter and shelter (halved egg cartons) and a slice of apple to provide food and moisture. The holding cages were placed on-site in a cool, shaded position away from disturbance and left throughout the day. About 2 h after dusk, animals were prepared for release within 10 m of the pitfall trap sites where they had been captured.

In early observations (2010 – 2015) animals were dusted with fluorescent pigments (Fiesta Daylight Pigments; Swada Ltd, London, UK) and the pigment trails followed using a UV black-light after release to facilitate detection of animals' foraging paths (Lemen & Freeman, 1985). In other early trials spool-and-line tracking was used (Boonstra & Craine, 1986). Here, a spool of fine 2-ply cotton thread that unwinds from the inside (cocoon bobbins, Coats Australia Pty Ltd., NSW) was glued to the nape of a *P. hermannsburgensis* using cyanoacrylic glue (“superglue”), and the free end of the spool tied to a shrub prior to the animal being released. The spools, weighing <5% of an animal's body mass, were shed after the animal had moved away a distance of 80–100 m and the entire length of the spool had paid out. Animals were followed several minutes after they had been dusted and released with fluorescent pigment, or released with the spool, to provide some time for them to move into cover and resume 'normal' behaviour. The trail left by the fluorescent pigment or the spool line was followed quietly on foot to enable the investigator to find the animal without causing undue auditory disturbance. In all situations a red torch (hand-held Dolphin Energizer or Ledlenser H7R head torch) was used to locate animals and minimise visual disturbance. This approach allowed the observer to get to within 2–3 m of focal animals without causing any apparent change in behaviour, although recent work does suggest that rodents have some capacity to detect red light illumination (Nikbakht & Diamond, 2021).

In later observations of *P. hermannsburgensis* (2016 – 2022), animals were captured and maintained over the course of a day as noted above, but were provided with a small cyalume fishing lure (4.5 mm × 29 mm; Nightlight, Aerostar Ltd) that was glued to an animal's nape using cyanoacrylic superglue. These lights emanate a weak green glow that lasts for 3–4 h before fading; pilot trials showed that the lure was usually shed by animals overnight or over the course of the next day. Although animals were still followed using red torchlight after their release near their point of capture, the weak green light was easier to find in the dark. Animals were likely able to detect these lights, but there was no evident effect on their behaviour when moving around or foraging.

In addition to using fluorescent pigments, spools-and-lines and cyalume lights, animals were sometimes detected during the course of the observer moving about on the dunes at night, and these animals were followed and observed when opportunities arose. Once detected, animals were followed using red torchlight and any foraging events observed. It was usually possible to see when animals had stopped and picked up a food item, except when animals had moved under dense cover, and it was often possible to identify what the food item was. Seeds could often be identified to species, with identification aided by the use of binoculars. Species identification was aided by a reference collection made by the Desert Ecology Research Group and by the observer's prior experience in seed identification. After animals had moved on from a foraging event, the site was inspected to confirm the identity of food items: sometimes parts of seed husks could be found, or intact seeds that had remained buried or otherwise not exploited by the forager provided confirmation. Green plants could usually be identified readily when animals stopped to feed on them, with confirmation made after the forager had moved on. However, invertebrates could be identified only at the time of capture, and the level of identification was usually coarse (e.g., spider, beetle). Descriptive notes were made on all foraging events, and times spent following animals were recorded.

Collection of stomach material and diet analysis

Specimens were collected over a period of 24 years on research trips to Simpson Desert. Some individuals had died in pitfall traps, others were collected during specific research projects (e.g., Predavec, 1997; Ricci, 2003; Gregory, 2008; Beh, 2011), others were collected opportunistically by land owners on Ethabuka and neighbouring properties to the immediate north of Ethabuka. All specimens were initially preserved in 10% formalin, then placed into 70% ethanol in specimen jars. There was a total of 186 *P. hermannsburgensis* stomachs. Eight specimens had no identification tags for date or location collected, and the stomachs of two specimens were empty, leaving 176 fully labeled and provenanced stomach-specimens from the study site. These were collected during different seasons and boom and bust periods between 1991 and 2014.

Previous research by Murray and Dickman (1994a) determined the minimum number of stomachs required to reliably determine dietary diversity of each seasonal population sample for *P. hermannsburgensis* to be 10 individuals. This minimum number was obtained by plotting the cumulative number of stomachs against the cumulative number of food categories that could be recognized in the diet, with the graph levelling off at $n = 10$ samples. The stomachs of the mice were removed and the contents analyzed; the contents of the intestines were not examined as these contents were usually too digested to allow reliable identification of food types.

Individual stomach contents were initially photographed using a Leica M205 C microscope, the contents were first washed with water to remove extraneous material such as hair or grit, and then washed through a 125 µm sieve to remove particles too small to identify (Murray & Dickman, 1994a), and then the contents were spread out on microscope slides and inspected in detail under 40x magnification. Contents and food fragments were photographed using the same microscope as previously and scored for presence or absence on a per-stomach basis.

Contents were initially separated into three major food classes of seed, non-seed plant material and invertebrate, with only the seed group identified to species. A reference collection of seeds collected previously at the study site was used to identify the seeds, with external characteristics such as seed coat used to determine seed species.

Statistical analyses

The direct observations of foraging were largely descriptive, but allowed tallies of three major food types to be made: seeds, invertebrates and green plants. Observations made using all three tracking methods were combined to provide an overall tally and to ensure that sufficient observations were available for analysis. A chi-squared goodness-of-fit test was used to determine whether the proportional frequency of items differed between these three major food categories. To test whether the representation of these food types differed by season or boom versus bust conditions, chi-squared contingency tests were employed. To test whether the dietary composition of the stomach samples differed by season or boom versus bust conditions, chi-squared tests were again used. However, because sample sizes were larger for stomachs than for the direct observations, further analyses were carried out to compare seasonal and boom and bust diets, with years as replicates. For these, I carried out permutational multivariate analysis of variance (*per*MANOVA), with 999 permutations, implemented in the vegan package in R version 4.2.2 (R Development Core Team, 2018). Sex was included as an additional factor. Statistical significance was accepted for any factors associated with a P-value < 0.05. If significant results were obtained, I used the similarity percentages (SIMPER) procedure to detect where differences occurred, again using the vegan package.

Results

Direct observations

Over the course of 24 field visits, 88 *P. hermannsburgensis* were followed and observed for a total of 163 hours. Twenty-three individuals moved quickly to sites under cover after release and stayed immobile for periods of at least 60–90 minutes, after which observations were terminated; 65 individuals were followed and observed for periods of 5–172 minutes (116 hours total) until they moved out of sight or observations were terminated. Of these 65 individuals, 53 were observed to consume food items; 38 individuals were observed to eat a single food item, and 15 stopped to eat between two and four food items, yielding a total number of 82 foraging observations where the main food type could be identified. There were at least 13 further occasions when animals appeared to stop and eat, but this could either be not confirmed or the food item not identified due to the orientation of the animal or obstructions that precluded a clear view; these incidences were excluded from further consideration.

When foraging, animals either moved slowly and apparently purposefully with the head close to the ground surface, or in a stop-and-start mode where they moved quickly from one site to another, usually less than 1 m apart, before slowing down and investigating the new site. Investigation took the form of sniffing at the ground and superficial digging, usually to a depth of no more than 1 cm but on two occasions to a depth of 2.5 cm, with the animal often remaining within a focal patch of no more than 100 cm^2 until moving to a new site. In 67 of the 82 foraging observations animals held the food item in their forepaws and ate it at the site where the item had been found; in 15 observations the food item was moved to a nearby site that provided more cover than that where the item had been found. Food items were carried in the mouth. Of the 116 hours that animals were in view, only 69 minutes were spent eating (mean ± SD: 50.49 ± 14.30 s per food item). *P. hermannsburgensis* appeared to be very vigilant for much of the rest of the time they were observed, either sitting immobile under cover, moving with ears erect, or pausing with the head up and one forepaw on the ground in an 'indecision-alert' posture. Animals were easily startled if the observer made a noise or if other minor disturbances were perceived, and either moved quickly under cover and remained immobile or adopted a vigilant stance until movement was resumed, usually several minutes later.

Of the food items that animals could be identified as consuming, 65 were seeds, 11 were invertebrates and six were leaves, stems or other green plant parts ($\chi^2 = 78.33$, 2 *df*, $P < 0.001$). There was no association between the frequency of food types eaten with either season ($\chi^2 = 7.84$, 6 *df*, $P = 0.25$) or boom and bust conditions ($\chi^2 = 0.23$, 2 *df*, $P = 0.88$) (Table 1). Because these tests included data from 15 individuals that had eaten 2–4 food items, hence violating the assumption of independence, I randomly selected only one of food items eaten by these 15 individuals and repeated the tests with a total $n = 53$. The results (not shown) were very similar to those when all observations were included.

Table 1. Frequency of items of three main food types observed to be eaten by sandy inland mice (*Pseudomys hermannsburgensis*), by season and boom or bust conditions, during observations at night in the Simpson Desert. Percentage values for each time period are shown in parentheses.

Food type	Spring	Summer	Autumn	Winter	Boom	Bust
Seed	14 (74)	12 (71)	21 (81)	18 (90)	27 (79)	38 (79)
Invertebrate	3 (16)	5 (29)	2 (8)	1 (5)	5 (15)	6 (13)
Green plant	2 (10)	0 (0)	3 (11)	1 (5)	2 (6)	4 (8)

Seeds that could be confidently identified as being consumed by *P. hermannsburgensis* included the grasses *T. basedowii* ($n = 8$) and *Aristida contorta* ($n = 1$); herbs and forbs *Goodenia cycloptera* ($n = 3$), *Haloragis gossei* ($n = 1$), *Trachymene glaucifolia* ($n = 4$), *Dicrastylis costelloi* ($n = 2$), *Newcastelia spodiotricha* ($n = 2$), *Trianthema pilosa* ($n = 2$), *Trichodesma zeylanicum* ($n = 1$), *Sclerolaena diacantha* ($n = 1$), *Sida fibulifera* ($n = 1$), *Crotalaria* sp. ($n = 1$); and shrubs *Grevillea stenobotrya* ($n = 11$), *Acacia ligulata* ($n = 3$), *A. dictyophleba* ($n = 2$), and *Dodonaea viscosa* ($n = 1$). Although it was not quantified, animals whose fluorescent pigment trails were followed often passed seeds on the soil surface during their foraging explorations without stopping to investigate or consume them. These included seeds of *Crotalaria* spp., *Eremophila* spp., *Eucalyptus* spp., *Senna pleurocarpa* and *Stylobasium spathulatum*, all of which are large and conspicuous, as well as patches containing many smaller seeds of species such as *Portulaca intraterranea* and *Euphorbia drummondii*.

Invertebrates that were eaten by *P. hermannsburgensis* included beetles (n = 2), lepidoptera (n = 1), spiders (n = 3) and an unidentified insect larva. Green plant material included the succulent leaves of *Calandrinia balonensis* (n = 2) and *Portulaca intraterranea* (n = 1), and the stems of small herbaceous *Trachymene glaucifolia* (n = 1) and *Oldenlandia pterospora* (n = 1) and fan flower *Scaevola depauperata* (n = 1).

Stomach content analysis

Seeds, invertebrates and green plant material were the main food categories recorded in the stomachs of *P. hermannsburgensis*, with seeds again predominating. Of the 176 stomachs that contained food material, 162 contained seed, 125 contained invertebrate and 39 contained green plant material (χ^2 = 73.29, 2 *df*, $P < 0.001$). If the stomach samples are included from the eight unprovenanced specimens, 169 samples contained seed, 129 contained invertebrate and 46 contained green plant material (χ^2 = 68.66, 2 *df*, $P < 0.001$). Seed was therefore the major component of *P. hermannsburgensis* diet with 92% of 184 stomachs (excluding the two empty stomachs) containing seeds, 70% containing invertebrates and 25% containing plant material. Overall, 62% of stomachs contained both seeds and invertebrates (Fig. 1). Plant material was never the sole food type in any stomach, and it always comprised less than 10% of the stomach contents.

Six seed species were identified, with 12 unknown species. The majority of the seeds identified were the grasses *Triodia basedowii*, which was identified in 81% of stomachs containing seed, and *Yakirra australiensis*, with dicotyledenous seeds of *Grevillea stenobotrya*, *Acacia dictyophleba*; *Trachymene glaucifolia* and *Ptilotus polystachyus* also identified. Green plant material could not be identified to species but included leaf, stem and root tissues, whereas invertebrates comprised insects and spiders; other invertebrate types were probably also present but could not be identified reliably.

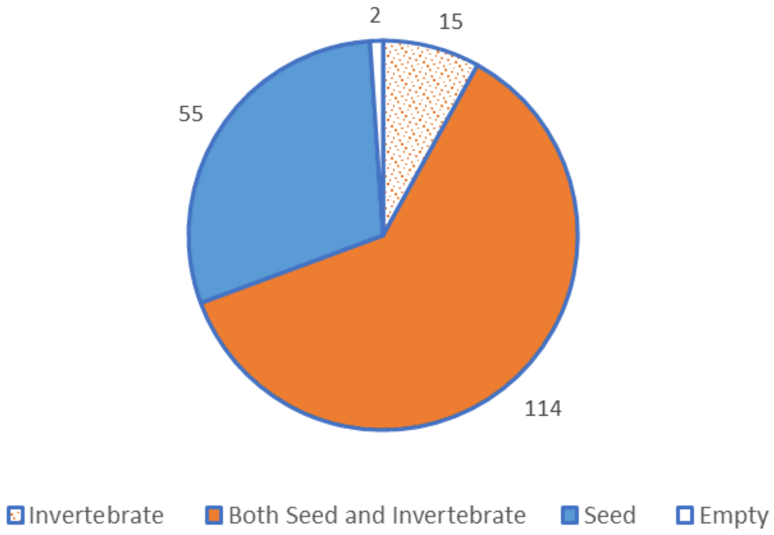

Figure 1. Frequencies of stomachs of sandy inland mice (*Pseudomys hermannsburgensis*) containing seeds alone, invertebrates alone and both food types together (n = 186).

More stomach samples were available from winter than from the other seasons (Fig. 2), but the distribution of food types eaten by *P. hermannsburgensis* did not differ between the seasons (χ^2 = 3.24, 6 *df*, P = 0.78) or boom and bust conditions (χ^2 = 5.94, 2 *df*, P = 0.051), although there was a trend for association in the latter test (Table 2).

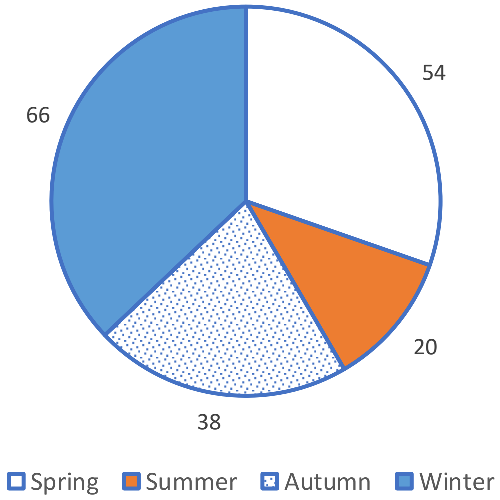

Figure 2. Number of stomach samples of sandy inland mice (*Pseudomys hermannsburgensis*) available for diet analysis, by season; n = 178, including two empty stomachs.

Table 2. Frequency of items of three main food types in the stomachs (*n* = 176) of sandy inland mice (*Pseudomys hermannsburgensis*), by season and boom or bust conditions, collected in the Simpson Desert. Percentage values for each time period are shown in parentheses.

Food type	**Spring**	**Summer**	**Autumn**	**Winter**	**Boom**	**Bust**
Seed	49 (49)	18 (55)	33 (44)	62 (52)	65 (58)	97 (45)
Invertebrate	36 (36)	13 (39)	31 (41)	45 (38)	33 (29)	92 (43)
Green plant	14 (14)	2 (6)	11 (15)	12 (10)	14 (13)	25 (12)

Averaging the dietary data between seasons over years confirmed the overall importance of seeds at all times. Invertebrates also were present in the diet in all seasons, with a particularly high frequency of occurrence (80%) of invertebrate material during autumn (Fig. 3). Green plant material was represented at low frequency in all seasons, with a small increase in autumn. There was, however, considerable variation between years in the representation of each food type in the diet (Fig. 3).

In further analysis, *per*MANOVA showed that there was no significant variation in the diet of *P. hermannsburgensis* by season (*df* = 3, *P* = 0.304), or by sex (*df* = 1, *P* = 0.872), and there was no significant interaction between season and sex (*df* = 3, *P* = 0.566). There was also no significant variation in diet between boom and bust periods (*df* = 1, *P* = 0.079). However, as the boom and bust comparison was close to being significant, a SIMPER analysis was run. This showed that there were significantly more invertebrates in the diet of *P. hermannsburgensis* during bust periods than during booms (boom average = 0.145, bust average = 0.583, SD = 0.164; and *P* = 0.041).

Figure 3. (On following page). Percentage seasonal occurrence (mean ± SD) of each of the three broad categories of food in the diet of sandy inland mice (*Pseudomys hermannsburgensis*) from 176 specimens collected in the Simpson Desert. (Note that error bars are symmetrical about the mean values, but for clarity are truncated where they would lie below 0% or exceed 100%.)

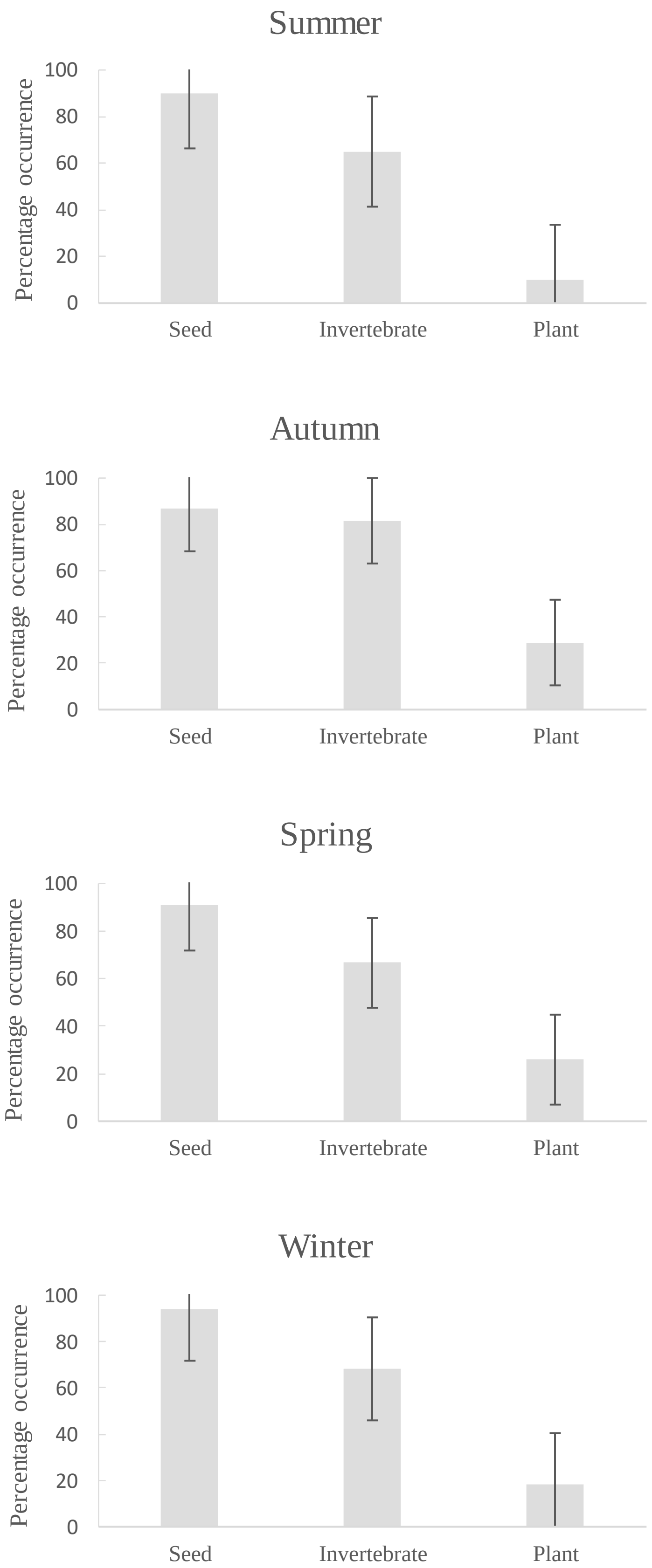

Figure 3. (See full caption above).

Discussion

Seed has been acknowledged as an important food resource for many desert-dwelling vertebrate and invertebrate species (Cloudsley-Thompson, 1991; Whitford, 2002), especially rodents (Brown, 1973; Reichman, 1975; Whitford, 2002). While invertebrates can be more beneficial than seed to consumers due to their relatively higher energy content, seeds provide other benefits such as requiring less energy expenditure to consume them (seeds are immobile and thus require less energy to acquire and consume), and contain different nutrients that may not be found in invertebrates; seeds also are often buried, creating seed banks that are an easy and consistent resource to be exploited by rodents (Reichman, 1975). Predavec (2000) was able to show the impact of seeds on *P. hermannsburgensis*: while supplementary feeding with sunflower seeds was unable to reverse a population decline, seed addition did slow the overall rate of decline. There is a relationship between seeds and rodents, as rodents rely on seeds for survival, and there is evidence from Gordon and Letnic (2016) that the fate of seeds, the seed bank and plant communities may be impacted by grainvorous rodents. The results in this study confirm that seeds are an important component of the diet of *P. hermannsburgensis*, with a substantial number of stomachs containing seeds. This result supports the findings of Murray and Dickman (1994a), who also concluded that seeds are a major component of the diet of *P. hermannsburgensis*, with over 50% of stomachs containing at least 70% seed.

The broad definition of an omnivore is that it is an animal that eats multiple different types of food or, more specifically, that the animal ‘shows no distinct, continuous preference for one particular food type, instead exhibiting a reliance on a number of different food sources’ (Murray *et al*., 1999). This study supports the classification of *P. hermannsburgensis* as omnivorous rather than granivorous, in agreement with the proposal of Murray and Dickman (1994a,b), with 13% of direct observations showing animals eating invertebrates and over half the stomachs analyzed containing both seed and invertebrate material. At least 11 of 16 desert-dwelling rodent species are confirmed or suspected to be omnivores in Australia; there may be more, but the diets of some species, such as the western pebble-mouse *Pseudomys chapmani*, are currently understudied or unknown (Murray *et al*., 1999). Being omnivorous would be advantageous to Australian desert rodents as rainfall can be highly unpredictable and this in turn will affect the predictability with which certain resources, such as seeds, will be available. It is notable that no Australian desert rodents are known to cache seeds for later use (Breed & Ford, 2007; Jackson *et al*., 2023), in stark contrast to heteromyid rodents in

North America and cricetid and sciurid rodents in other parts of the world (Vander Wall, 2010). This presumably reflects uncertainty that a seed cache, even a large one, may be able to sustain Australian desert rodents through long bust periods. However, by exploiting invertebrates and green plant material, rodents likely increase their chance of survival and decrease the risk of starvation compared to their prospects if they were limited to just seeds in their harsh and unpredictable arid environment (Morton, 1983; Kelt *et al.*, 1996).

Flexibility in switching between the main food groups was less evident than initially expected, but there was some evidence ($P = 0.041$) that invertebrates were taken at higher frequency in bust compared to boom periods. This most likely reflects food resources, specifically seeds, being scarce during bust periods, as shown by Predavec (1994) and Ricci (2003), so *P. hermannsburgensis* supplement their diet with invertebrates. Although rainfall can positively affect some invertebrate groups, such as ants (Gibb *et al.*, 2022), populations of many taxa respond negatively to rainfall or appear unaffected by it, and are thus relatively more available during dry bust periods than during booms (Kwok *et al.*, 2016). A shift towards increased importance of invertebrates in the diet has been observed previously by Murray and Dickman (1994a), except that these authors saw this shift during autumn; their assumption was that dietary shifts are due to the relative availability of different resource groups and thus that the increase of invertebrates in autumn diets could reflect increased availability of invertebrates and/or a decline in seeds. We also found an apparent increase of invertebrates in the diet of *P. hermannsburgensis* in autumn (Fig. 3), but the significance of invertebrates only became apparent when stomachs were separated by boom and bust periods. As the effect of boom and bust was close to being significant in PERMANOVA, a follow-up SIMPER analysis revealed invertebrates to be eaten significantly more frequently in bust periods ($P = 0.041$). The suggestion that temporal shifts in diet reflect the relative availability of different foods (Murray & Dickman, 1994a) seems appropriate, but awaits further confirmation by studies that simultaneously monitor food availability and foods eaten.

The present study had a number of strengths and weaknesses. On the one hand, diets could be studied over a long time period owing to the availability of specimens that had been collected across boom and bust periods and from all four seasons over 24 years. Early studies by Watts (1970), Morton (1979) and Watts and Morton (1983) classified *P. hermannsburgensis* as granivorous but used small sample sizes of only 4–6 animals. Murray and Dickman (1994a) showed that larger sample sizes were needed to reliably classify the species' diet, and also concluded that if samples were collected only in winter or summer it could be assumed—

erroneously—that the species is primarily granivorous. In this study, regardless of season (Fig. 3), invertebrates appeared to play an important role in the diet of *P. hermannsburgensis*, with sample sizes of 20–66 between different seasons showing substantial contributions of invertebrates to the diet at these times.

On the other hand, this study had some key limitations. In the first instance, with direct observations there are a few limitations such as the accuracy in identifying the seed species being consumed as the observing is a far enough distance to not disturb the animal which could make misidentification of seeds possible due to the small size and distance; another limitation is the observation may have bias to animals that are ‘bold’ and are willing to forage in human presence, animals that were not observed ‘shy’ that hid could potential have a different food preference. By using stomach contents this may reduce the bias for shy and bold animals as it is assumed that the mice are caught randomly, but many specimens were caught in traps it could be there are certain mice that avoid traps and so the contents being analysed could be biased to animals easily caught in taps; only a gross dietary analysis could be carried out on the *P. hermannsburgensis* stomachs, with only the presence or absence of the three major food classes of seed, invertebrate and plant material (non-seed) recorded. Most of the specimens were old and the poor state of preservation of much of the stomach material meant that the most reliable level of identification was at the coarse food group level. I did attempt to identify seeds to as fine a level as possible where these had been preserved well, but neither invertebrates nor green plant tissues were identified further. Future studies using older specimens may find it useful to perhaps be to weight the samples in the analyses based on time, which would account for the effects of decay over time on stomach contents. It would be advantageous to conduct more-detailed dietary analyses by scoring the relative abundance of each specific food item by estimating its percentage occurrence in fresher or better preserved samples (Murray & Dickman, 1994a), or to explore the utility of DNA-based mini- or meta-barcoding techniques to identify the full range of dietary items (e.g., Rodrigues *et al*., 2020). These latter techniques have the advantage that they can be used on faecal samples. Secondly, this study lacked spatial variability, as all specimens were collected on or near to Ethabuka, in the north-eastern Simpson Desert. *P. hermannsburgensis* is found across Australia in semi-arid and arid areas, often in hummock grasslands, but also in other habitats such as mallee shrublands and acacia woodlands (Watts & Aslin, 1981; Predavec, 1994; Kutt *et al*., 2004; Breed & Ford, 2007). There could be potentially much greater variation in the diet of *P. hermannsburgensis* from different regional areas. For example, while a flexible diet is selectively advantageous for survival in unpredictable desert conditions (Kelt *et al.*, 1996; Morton, 1993), in semi-arid areas or areas where rainfall is more frequent and predictable, *P. hermannsburgensis* could be potentially more granivorous or herbivorous.

Interestingly, 38 specimens had worms in their stomachs. There has been extremely limited research on parasites in Australian desert rodents (Weaver & Smales, 2012), and the stomach worms could not be further identified here. It is unclear whether these worms may have affected the health or behaviour of the infected animals, and studies of the prevalence and incidence of species of endoparasites remain to be conducted in both *P. hermannsburgensis* and other species of Australian desert rodents.

In conclusion, this chapter confirms that seeds play an important role in the diet of *P. hermannsburgensis* at all times of the year, and during boom and bust periods, at least in the sand dune environment of the Simpson Desert, but also supports the reclassification of this species by Murray and Dickman (1994a) as omnivorous owing to the contribution that is made to the diet by invertebrates and, to a lesser extent, green plant material. The direct observations of foraging by *P. hermannsburgensis* also provided some novel insights and intriguing questions about how animals find their food and the factors that affect the selection of food items. For example, animals spent only 0.99% of their time while active (69 of 6960 minutes) actually eating, with observations suggesting that they usually remain close to, or under, cover and that vigilance takes up a considerable portion of each animal's time budget. Is the risk of predation a constraint on foraging? Animals also appeared to dig only superficially for food items and clearly ignored seeds that were readily available on the soil surface before going on to select other, apparently similar, seeds. These observations bring into question the extent to which *P. hermannsburgensis* digs for food and the cues that it uses to select certain foods but not others. These questions are explored in subsequent chapters in this thesis, with a focus on the benefits and costs of exploiting the seed component of the diet.

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Chapter 4. Foraging and seed selection of rodents under different risks of predation

Abstract

Risk of predation often influences where prey animals forage, when they are active, their allocation of time to vigilance or other anti-predator behaviours, and hence the amount of food that they consume. Predation risk also can be expected to influence the dietary composition of foragers, but this response to predation has been little studied. Here, animals foraging in patches perceived to be safe from predation were predicted to have sufficient time to be selective in their choice of prey types, whereas animals foraging in risky patches were predicted to exhibit limited or no selectivity owing to their need to quickly consume any prey types they encountered. To test these predictions, the activity of predators of the sandy inland mouse (*Pseudomys hermannsburgensis*) was monitored at a study site in the Simpson Desert, central Australia, and safe and risky foraging microhabitats in the landscape were identified; respectively, these were patches under the cover of spiky-leaved spinifex (*Triodia basedowii*) hummocks and patches of open sand. Cafeteria-style trays containing spinifex and *Grevillea stenobotrya* seeds (highest quality seeds, most preferred by *P. hermannsburgensis*), *Eremophila macdonnellii* (least preferred) and *Goodenia cycloptera* and *Trachymene glaucifolia* (intermediate preference) were placed in open and sheltered spinifex microhabitats to determine the effects of predation risk on seed choice by the mice on five occasions. Results indicated initially that mice selected and consumed mostly their preferred seeds in sheltered microhabitats but took all seeds equally in the open, as predicted. However, when predator activity decreased the risk of foraging in the sheltered and open microhabitats became similar, and microhabitat became a less significant influence on seed choice. A switch in consumption from seeds of *T. basedowii* to *G. stenobotrya* was observed over time, perhaps reflecting changes in seed quality or familiarity of the rodents with seeds in the soil seed bank. Overall, *P. hermannsburgensis* appears to be sensitive to predator presence and predation risk, balancing where they forage and what they consume according to the degree of risk they perceive. These novel results provide specific insight into how predation risk affects diet choice as well as general support for foraging theory.

Introduction

In the previous chapter direct observations and stomach content analysis showed the sandy inland mouse (*Pseudomys hermannsburgensis*) to be omnivorous, but with seeds forming the major part of the diet. The direct observations also showed that animals spent very little of their active time eating, appeared to be very vigilant when moving, and fled rapidly to seek cover if startled, suggesting that they may be sensitive to disturbances such as the risk of predation. Small rodents often fall prey to larger vertebrate predators, and must therefore balance the time and energy they expend on foraging with the time and energy needed to avoid becoming prey themselves. The trade-off between these two imperatives, both of which have profound effects on fitness, can result in dietary compromises if individuals forage for shorter times, in places where food is less available, or accept poorer quality food to reduce their risk of predation. This chapter investigates whether risk of predation affects food choice in *P. hermannsburgensis*.

Predation affects prey species directly by removing prey animals from the population, but also has indirect impacts by altering prey behaviour (Brown *et al.*, 1988; Kotler *et al.*, 1991; Bleicher, 2017). Predation risk can constrain access to food as prey shift their activity to less risky time periods and/or less risky microhabitats, with examples documented from a wide range of vertebrate and invertebrate consumers (e.g., Brown *et al.*, 1988; Rypstra *et al.*, 2007; Mukherjee *et al.*, 2014; Doherty *et al.*, 2015). In different areas and during different periods/seasons food varies in availability and quality, complicating the decisions that animals must make about balancing food acquisition with predation risk. In many theoretical and empirical studies the outcomes of these decisions have been shown to be consistent with foraging theory, which predicts broadly that animals will choose the option that maximises the objective (usually energy intake), subject to constraints (usually predation, in studies investigating extrinsic constraints) (Stephens *et al.*, 2007).

Most prey species balance increased vigilance, use of less risky microhabitats and decreased time spent foraging for food to reduce their chances of encountering a predator (Brown, 1999; Brown *et al.*, 1988). Rodents exemplify these behaviours, often seeking refuge in structurally complex habitats with high vegetation cover to reduce the chance of encountering predators, which are often more likely to occur in open areas (Doherty *et al*., 2015; Laundré *et al*., 2017), or conversely increasing vigilance behaviours if in risky habitats to increase the chance of detecting a predator (Osada *et al*., 2015; Fardell *et al*., 2020). Rodents will often spend more time and consume more food in closed areas with abundant cover (lower risk of predation) compared with open, bare and riskier areas (Thompson, 1982; Kotler, 1984; Kotler *et al*., 1994; Dickman *et al*., 2010). Prey animals use varied indirect cues to assess predation risk, such as habitat complexity, as well as direct cues such as the sight, sound or smell (e.g., urine or faeces) of a predator, with some research suggesting that indirect cues are more informative to prey animals if they are subject to predation from a diverse suite of predators (Orrock *et al*., 2004). Despite the effectiveness of anti-predator behaviours, however, their overuse can negatively affect the fitness of prey animals by causing them to reduce the time they spend foraging and/or to forage in areas of decreased quality or productivity that will often be close to refuges and escape paths (Orrock *et al*., 2004).

In the case of *P. hermannsburgensis*, predation may have a greater negative effect on population numbers than reduced food resources, as populations of this species have been observed to decline faster than their food resources when in the presence of predators (Dickman *et al*., 2010). This study seeks to determine whether the risk of predation perceived by animals is translated into differences in foraging behaviour and dietary preferences. Questions about diet choice under varying levels of predation risk have been posed much less often than questions concerning amounts of food eaten (e.g., Godin, 1990; Sih, 1993), but have been addressed in theoretical studies comparing 'fallback' (inferior quality) foods compared with preferred foods (Yeakel *et al*., 2020). However, questions about diet choice are particularly relevant for omnivorous foragers such as *P. hermannsburgensis* that must make decisions about which food types to select among many that may be available in an environment that poses different levels of predation risk. We hypothesize that animals encountering food resources in patches associated with high predation risk will spend less time foraging there and will accept inferior quality food items, as compared with animals that encounter the same food resources in patches associated with a lower risk of predation that will forage for longer and preference the consumption of higher quality food items over those of lower quality.

To effectively test this hypothesis, several requirements need to be met. In the first instance, it is necessary to know which predators pose most risk to the study species, and to then identify patches in the landscape where the risk of predation from these species is relatively high and relatively low. In the immediate study area (see below), *P. hermannsburgensis* is preyed upon by native species such as barn owls (*Tyto alba delicatula*), sand goannas (*Varanus gouldii*), brush-tailed mulgaras (*Dasycercus blythi*), and the dingo (*Canis dingo*/*familiaris*), with predation pressure being relatively light or sporadic due either to the local rarity of these species (*T. a. delicatula*, *D. blythi*, *C. dingo/familiaris*) or the difference in timing of diel activity (*V. gouldii* is diurnal, *P. hermannsburgensis* is nocturnal) (Chen *et al*., 1998; Kutt *et al*., 2020; Dickman *et al*., 2022). However, predation pressure on *P. hermannsburgensis* in the study area is much heavier from the introduced European red fox (*Vulpes vulpes*) and feral cat (*Felis catus*); it remains consistent between boom and bust periods and across different seasons (Spencer *et al*., 2014a, 2017), exerting downward pressure on populations of the mice (Mahon, 1999; Greenville *et al*., 2017). A reliable test of the above expectation should therefore confirm that both foxes and cats are present and active in the study area.

A second requirement is that patches of high and low risk from the identified predators can be specified, or created, in the foraging landscape of the study species. There are several ways to do this. For example, models of the prey species can be placed in different patches, or microhabitats, in the landscape, and attack rates by predators recorded (e.g., Paluh *et al*., 2014; Hernández-Agüero *et al*., 2020). In the study area used here, Tesoriero (2011) used toy mice deployed in five different microhabitats in the Simpson Desert, and showed that foxes and cats were at least 10-times more likely to attack models on open sand compared with those that had been set under the cover of spinifex (*Triodia basedowii*) hummocks. Another approach uses the giving-up density (GUD) technique. The GUD approach provides a useful way for researchers to experimentally manipulate patch quality to test predictions arising from foraging theory, and is often set up using simple dishes or trays containing food items mixed into a substrate. These are set in the environment where foragers have some chance of encountering them, and the GUD is then measured simply as the amount of food left at the end of a foraging bout (Brown & Alkon, 1990). This technique can be used to quantify many different characteristics of foraging behaviour, such as perceived food availability, harvesting costs, missed opportunity costs and other variables such as physiological constraints (Shaner *et al*., 2007; Bedoya-Perez *et al*., 2013). Of the many uses for GUDs, however, perhaps the most commonly exploited use has been to study how predation risk is perceived by foragers (e.g., Kotler & Brown, 1988; Shaner *et al*., 2007; Dickman *et al*., 2010). Research using giving-up densities on rodents (e.g., Powell & Banks, 2004; Pastro & Banks, 2006; Bedoya-Perez *et al*., 2013) has shown generally that rodents spend less time at foraging patches in response to both direct (predator presence) and indirect sources of predation risk such as the openness of habitat. Studies based on measuring foraging and movement indicate that small mammals spend less time in open habitats (Jacob & Brown, 2000), and Powell and Banks (2004) confirmed that giving-up densities of mice (*Mus musculus*) were consistently higher (fewer visitations) in open compared with sheltered microhabitats. Quadrupedal rodents in general prefer to forage in areas with more cover, such as near shrubs, whereas bipedal rodents forage preferentially in the open as they use speed to escape oncoming predators (Randall, 1993). Previous GUD studies on *P. hermannsburgensis* have shown that animals forage for longer and consume more food in closed, structurally complex microhabitats than in open, more risky habitats (Dickman *et al*., 2010; Doherty *et al*., 2015), and also avoid GUD dishes that have been experimentally tainted with cat odour (Spencer *et al*., 2014b).

A final requirement for testing our initial expectation is that the forager can recognise and discriminate different food items, such as different seed species, selectively consuming some over others. There are many factors that influence the preference for different native seed species by desert rodents, such as seed size, energy content, macronutrients, handling time, and the amount of available free water (Kelrick *et al*., 1986; Murray & Dickman, 1997; Wang & Yi, 2022). Direct observations of *P. hermannsburgensis* suggested that seeds such as *T. basedowii* and *Grevillea stenobotrya* may be selected (Chapter 3), and cafeteria trials suggest further that these mice may select seeds with the highest free water content, although other factors such as nitrogen content, seed shape, and hardness are likely also to be important (Murray & Dickman, 1997).

With these considerations in mind, we can refine our initial expectations and predict that 1) *P. hermannsburgensis* will perceive a lower risk of predation from foxes and cats near spinifex hummocks than in the open, and therefore spend more time at foraging patches in these sheltered microhabitats than in the open. GUDs should be lower at foraging patches near spinifex than in the open if this prediction is supported. Then, if foraging patches are set up with seeds that vary in quality (water and energy content), we predict that 2) animals that visit patches near spinifex will have sufficient time to select the higher quality seeds, whereas animals that visit patches in the open should show little or no seed-selectivity as they have less time to be selective and must 'eat on the run'. These predictions are tested in this chapter and further explored in the next.

Methods

Study site

Research was conducted on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E). The landscape has long, parallel sand dunes up to 8 m high and 0.5-1 km apart with hard claypans forming between the dunes (Wardle *et al*., 2015). The major vegetation on dune sides and swales is spinifex (*Triodia basedowii*), with perennial shrubs such as *Crotalaria* spp., *Tephrosia rosea* and *Grevillea* spp. dominating the dune crests; in the swales there are also stands of gidgee trees (*Acacia georginae*) (Wardle *et al*., 2015). Ephemeral grasses and herbs provide ground cover after rain.

The annual rainfall varies greatly between dry and unproductive ‘bust’ years and years with extreme rainfall or flooding that drive ‘boom’ events. The heaviest rainfalls occur mostly in summer with occasional heavy rains that fall locally or regionally at other times (Greenville & Dickman, 2005; Dickman *et al.,* 2010). Over 94 years an average 199 mm/year of rain was measured at Marion Downs (a station located 120 km from Ethabuka), but rainfall can differ significantly between years as 214.2 mm of rain fell in 1999, and well above average rain (496.6 mm) in 2000 (Dickman *et al.,* 2010). Rainfall in arid Australia can be variable in space and time and measurements recorded at a station over 100 km may not accurately reflect the actual rainfall of the site. For example, Letnic & Dickman (2005) found significant temporal and spatial variation in rainfall between three sites in the Simpson Desert that were spaced 50 km apart. Thus, while measurements from a distant weather station may not show the exact rainfall of the area studied, they provide a good reference for the general weather pattens in the area and can be used to determine boom and bust periods which generally occur over the whole desert system and not just in isolated locations.

Temperature varies widely depending on season with average daily temperature exceeding 40°C in summer and minima falling below 5°C in winter (Greenville *et al.*, 2012).

Study species

This study focuses on the foraging behaviour of the sandy inland mouse (*Pseudomys hermannsburgensis*), a nocturnal omnivore that includes seed as a major part of the diet (Chapter 3). In the study area it forages mostly on the sides and in the swales of dunes, and seldom near the dune crests (Predavec, 1994, 1997). The main predators of *P. hermannsburgensis* throughout its wide geographical range are the feral cat and red fox (Dickman, 1996; Risbey *et al.*, 2000; Glen & Dickman, 2005; Johnston *et al.*, 2007); as noted above, these are also the major predators of *P. hermannsburgensis* in the study area (Spencer *et al.*, 2014a, 2017).

Tests of the predictions: prediction 1

Predator activity

To confirm the presence of feral cats and red foxes during the course of this study (2010–2015), three methods were used. Firstly, to gain a regional perspective on predator activity, two camera traps (Moultrie i40) were set immediately south and north of the site where the foraging experiments were carried out (see below), and 22 additional camera traps (Moultrie i40) were set over an area of ~8000 km^2 at sites east, west, north and south of the experimental site. All cameras were set on unmade vehicular tracks on stakes at a height of 1.5 m, and angled down at 10° to ensure that the field of view encompassed the tracks (Greenville *et al.*, 2014). Deployment of cameras on tracks followed the findings of May and Norton (1996) and Mahon *et al.* (1998) that tracks are used frequently by both feral cats and foxes. Cameras were downloaded 3–4 times a year, images screened for cats and foxes, and data written to EXIFPro 2.0 (Kowalski & Kowalski, 2012) for storage and analysis, as described by Greenville *et al.* (2014). To increase the likelihood that images of animals were independent, the cameras were programmed to trigger after 1-min delays, and photographs of potentially the same animal within a further 2 mins were discarded from analysis. The resulting gap of at least 3 mins between photographs was assumed to produce independent photographic events (see Greenville *et al*., 2014).

Secondly, to gain more local insight into predator activity at the experimental site at the time when foraging experiments were being run, spotlighting and sand transecting were carried out. For spotlighting, two observers sat on a vehicle moving at ~15 km/h along an unmade vehicular track that ran close to the experimental site, and counted cats and foxes observed on either side of the track using 100-W Lightforce spotlights. The spotlight transect ran for ~15 km, with 7 km to the south and 8 km to the north of the experimental site, and was completed 2–4 h after sunset. One or two spotlight transects were run on each field trip when the foraging experiments were carried out. For sand transecting, three transects (each 50 m long × 1.0 m wide) were constructed at four sites surrounding the site where the foraging experiments were carried out. One transect in each set of three was established in the swale, the next was set parallel on the dune side 50 m away, and the third was set near the dune crest a further 50 m away. Each transect was raked and then dragged using a hessian sack half-filled with sand to create a smooth surface on the sand that was suitable for capturing the prints of any animals that walked upon them. Transects were set by day and checked—and reswept as necessary—on three consecutive mornings. Predator footprints were recorded as presence or absence on each transect using field guides to confirm identification (Moseby *et al*., 2009). In the event of uncertainty, prints were photographed and reviewed later.

Patches of high vs low predation risk for prey

In an initial attempt to directly manipulate the degree of risk that might be perceived by *P. hermannsburgensis* at foraging patches, *P. hermannsburgensis* were captured at the study site and given the choice of foraging in the presence or absence of cat odour within a modified choice chamber apparatus (Appendix 1). Although initial results showed that animals fed less at food dishes in the presence of cat odour compared to odourless control dishes, the use of cat odour cues was not pursued. The effect of the odour was ephemeral, lasting no more than one night, and the logistical challenge of transporting sufficient materials bearing cat odour at the required temperature (< 0°C) to a frequently hot and remote desert site made the use of predator odour impractical (Appendix 1). Hence, indirect approaches to creating foraging patches of high vs low predation risk were explored.

Based on previous research, vegetation cover was considered to be a reliable indirect cue for predation risk. In particular, hummocks of spinifex grass were considered likely to represent safe patches where *P. hermannsburgensis* could forage, and open sand sites to represent sites of elevated risk. Two methods were used to quantify potential differences in the degree of risk in these two microhabitats. Firstly, mouse models were set out in pairs under spinifex hummocks and on open sand > 1 m from any cover, and the sandy substrate in a 50 cm radius around each model was lightly swept so that the footprints of visiting predators could be identified. The models were toy mice with synthetic fibre 'fur', 7.5 cm long (including a short tail) and 2.5 cm wide ('Night Creatures': Petbarn Ltd, Sydney). The models approximated the size of *P. hermannsburgensis* and, to ensure that their odour also resembled that of real animals, the models were placed in calico bags that had been used earlier the same day to hold captured *P. hermannsburgensis* and which also contained scats from the captured animals. The models were set out in the field at least six hours after placement in the calico bags to allow sufficient time for odour to be imbued in the models' fur. The models in each pair were set out no more than 5 m apart to ensure that a passing predator would have an equal chance of encountering either or both models, with each pair separated by > 1 km from the next along unmade access tracks in the study area to reduce the chance of multiple visits by the same predator. Each model was suspended 0.5–1 cm above the ground using fine cotton thread tied to an overhead structure to allow wind-driven movement to occur, simulating (to a degree) the movement that might be expected of a living rodent. Predator visits to the models could be recognised by bite marks or by complete removal of the models, with the identity of the predator confirmed by footprints at the site. Missing models were replaced, and the sandy substrate reswept, after any predator visit. In total, 15–24 pairs of models were set on two occasions, in November 2010 and November 2014, and checked for 5–8 consecutive mornings to record whether predator visits or attacks had occurred.

Secondly, the traditional giving-up density (GUD) technique was used. For this, I mixed either 10 or 20 quartered peanuts into 200 ml of sifted sand in plastic dishes (14 cm diameter × 5 cm deep) and presented the dishes to foragers in the two microhabitats, open sand ('open') and under spinifex ('closed'), at sites within 1 km of the site where the foraging experiments were carried out. Between 10 and 12 pairs of dishes were set up, one in each microhabitat, usually 2–5 m apart, with each pair of dishes at least 20 m apart to ensure a degree of spatial independence (Dickman *et al*., 2010). The dishes were half-buried in the sand and the sand in a 10 cm radius around each dish was then smoothed so as to capture the footprints of visiting small mammals. These were identified using field guides (Moseby *et al*., 2009) as well as reference photographs of the tracks left by animals that had been captured and later released as part of parallel studies (Dickman *et al*., 2010, 2014). The tracks were possible to differentiate between spinifex hopping mouse (*Notomys alexis*), dasyurids (*Sminthopsis* sp.) and *P. hermannsburgensis*, which were the most common small mammals in the area. While other species have been previously found in the area with similar footprints that can be difficult to distinguish, such as the desert mouse (*Pseudomys desertor*) and house mouse (*Mus musculus*), local trapping not far from the experimental site indicated that populations of the other two mouse species were very low. Previous trapping records indicate further that these species are often at very low numbers during a bust period, making it very unlikely that any footprint that was not that of *P. hermannsburgensis*; photographs were also taken that reconfirmed footprint identification.

If a dish was visited, the nuts were replaced and the sand smoothed again. GUDs (i.e., nuts left after a night's foraging) were counted and recorded each morning for 3–4 consecutive mornings. GUD trials were run in November 2010, May 2011, June 2014, April 2015 and September 2015 to coincide where possible with the seed foraging experiments set up to test prediction 2 (see below).

The results of the model mouse trials showed that feral cat and red fox activity is much greater in open than in spinifex-covered microhabitats, and the GUD trials confirmed further that *P. hermannsburgensis* perceives foraging patches in open sand to represent sites of high risk (i.e., GUDs were high) and foraging patches under spinifex hummocks to represent relatively safe sites (GUDs were low). These results, presented in detail below (see Results) informed the design of experiments to test prediction 2.

Tests of the predictions: prediction 2

Assessing seed quality

From the direct observations of animals foraging and the seeds they were observed to eat (Chapter 3), as well as the results of seed preference trials presented by Murray and Dickman (1997), five seed species were selected to test prediction 2. These were *Triodia basedowii* (spinifex), *Grevillea stenobotrya*, *Eremophila macdonnellii*, *Goodenia cycloptera* and *Trachymene glaucifolia*. These five species were found commonly in the study area and would thus have been familiar to foraging animals. From previous work, *T. basedowii* and *G. stenobotrya* seeds were expected to be preferred by *P. hermannsburgensis* based on their likely water and energy contents and net energetic return to mice, while *E. macdonnellii* was expected to be least preferred; *G. cycloptera* and *T. glaucifolia* were expected to be of intermediate preference. To quantify the energy and water contents of these seed species, fresh seed was collected in the field and samples returned to the laboratory for testing. The water content of seeds was determined by drying seeds individually or in small batches at 100°C to constant weight (Murray & Dickman, 1997), while the energy content of the seeds was determined using a bomb calorimeter (model PARR 1109A). Calorimetry followed manufacturer instructions (1109A Semi-micro Oxygen Instruction Manual by Parr Instrument Company Revision 01/29/2010;

https://www.parrinst.com/products/sample-preparation/oxygen-combustion-bombs/semi-micro-oxygen-combustion-bomb-model-1109a/documents/). In brief, ~0.22 g of dry seed was placed in the calorimeter crucible, the fuse added to the crucible lid, and the crucible assembly placed into a moistened bucket prior to ignition of the sample. The resultant temperature change allowed calculation of the energy yield via the formula: energy equivalent × temperature change (-fuse weight left)/ mass. Between three and six replicates were used in energy and water content analyses.

Cafeteria seed choice experiments

With 'safe' and 'risky' microhabitats identified as noted above, the five seed species were presented to foraging rodents in ‘cafeteria’ style choice experiments in swale and lower dune sites throughout the study site where *P. hermannsburgensis* spend most time active. Measured weights of each seed species (~0.5 g) were placed separately into small (5 cm diameter, 1 cm deep) plastic Petri dishes, with the five Petri dishes in turn set out on a larger (30 cm diameter) seed plate. Thirty-six seed plates were set up in open sand microhabitats (high predation risk), paired with 36 more seed plates under spinifex hummocks (low predation risk). Pairs of plates were 3–5 m apart, with each pair separated by at least 20 m to ensure a degree of spatial independence, as in the GUD experiments. The sand in a radius of 10 cm was smoothed so that the footprints of visiting rodents could be captured and the identity of the foragers recorded. To reduce the chance of ant attack on the seed dishes, the seed plates were elevated ~5 cm above the sand surface on wooden tripods, with the legs of the tripods smeared with a mixture of Vaseline and Coopex insecticide powder (Bayer Ltd, Pymble, Sydney). Pilot trials confirmed that *P. hermannsburgensis* were readily able to access the elevated plates. The seed plates were set up in the late afternoon and checked at first light to reduce the chance of disturbance by birds for 5–8 consecutive nights on five field trips between 2010 and 2015. If a plate had been visited by a small mammal, the footprints were identified as noted above and all seed dishes on that plate were removed and the remaining seeds weighed. Seed plates were checked and any seeds that had been consumed were replaced for each successive night until the conclusion of the field trip.

Because the seed dishes were necessarily open for *P. hermannsburgensis* to be able to visit them, the seeds could potentially lose mass from dehydration or increase in mass due to high humidity. Nights with wind could also blow seeds away. To account for any changes in seed mass not caused by rodent foraging, a wire mesh cage was placed over two seed plates, one in the open and one under spinifex, and seeds in all dishes on both plates reweighed each morning. As the wire mesh prevented rodent access, any overnight change in seed mass could be attributed to environmental factors rather than to foraging losses.

Statistical analyses

Predator activity from the camera traps, spotlighting and sand transects is presented simply as the tally of feral cats and red foxes detected during the periods when these methods were implemented. Seed water and energy content are also presented simply as means ± SD for the five seed species that were used. Predator attacks on model mice were tallied and any differences in numbers of attacks by feral cats and red foxes between the two microhabitats (open sand and under spinifex) were assessed using chi-squared goodness-of-fit tests. To evaluate differences in GUDs for *P. hermannsburgensis* between the two microhabitats, GUD values were averaged for each dish visited by this species over the 3–4 nights that the dishes were set. Following Dickman *et al*. (2010), results were omitted from dishes that had not been visited or had been visited by other rodent species (notably the spinifex hopping-mouse, *Notomys alexis*) or other foragers such as birds. The GUDs were then compared between the two microhabitats using 1-factor analysis of variance (ANOVA).

To assess seed selection in the cafeteria seed choice experiments, the response variable of interest was dry seed mass removed by *P. hermannsburgensis*. For this analysis, data from seed plates that had been visited by the target species were used, and any plates that had not been visited or had been visited by other species of rodents, as determined by footprints on the smoothed sand around the plates, or had been otherwise disturbed, were omitted from analysis. The mass of each seed species removed by *P. hermannsburgensis* was averaged over the nights that the plates were in place, with these weights adjusted after correction for weight gains or losses in each seed species that had been set up on the control plates; these seeds were not available to foragers but had been exposed to prevailing environmental conditions through each night. The corrected mass of each seed species removed was compared between the open sand and under spinifex microhabitats using 2-factor ANOVAs.

Before ANOVAs were carried out on the GUD and seed choice data, Levene's test was employed to check for equality of variances (Quinn & Keough, 2002). All sets of GUD data, but not the seed choice data, were heterogeneous, and neither log(x + 1) nor arcsine nor proportional transformations were able to homogenise them. Following the recommendations of Underwood (1997) and the previous practice of Dickman *et al*. (2010), ANOVAs were therefore run on untransformed data and statistical significance was accepted when $\alpha \leq 0.01$. Statistical significance was accepted at $\alpha \leq 0.05$ in all other tests. Data are means ± SD unless otherwise stated, and all tests used JMP 16.0 (Goos & Meintrup, 2015; SAS, 2020).

Results

Prediction 1: Predator activity and use of microhabitats

Over the duration of this study 2,842 independent images of predators were recorded, comprising 1508 images of feral cats, 903 images of red foxes and 431 images of dingoes. The three predators were active across the broader study region, including to the immediate south and north of the main study site (131 feral cat images, 80 red fox images, 32 dingo images). The numbers of predators spotlighted and transects with predator tracks are noted below with the seed choice experiment results for each occasion these experiments were run.

Both feral cats and red foxes attacked more model mice in open than in spinifex-covered microhabitats in both November 2010 and November 2014 (Table 1). Most models were bitten or torn off their cotton suspension lines by these predators, or otherwise disturbed (e.g., feral cats urinated on or close to mouse models on two occasions). Seven models visited by feral cats were removed entirely, as were six models visited by red foxes. Models were also attacked by dingoes, Australian bustard (*Ardeotis australis*) and unidentified corvids, but in numbers that were too low to analyse. GUD results for the two microhabitats are noted below with the seed choice experiment results.

Table 1. Frequencies of attack by feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) on model mice in two microhabitats on two trial occasions in the Simpson Desert.

	November 2010		**November 2014**	
Microhabitat	Feral cat	Red fox	Feral cat	Red fox
Under spinifex	2	1	4	2
Open sand	19	15	15	12
χ^2	13.76	12.25	6.37	7.14
P	<0.001	<0.001	0.012	0.008

χ^2 values were derived from goodness-of-fit tests associated with 1 *df*.

Prediction 2: Seed choice experiments

Seed quality.—The five seed species used in the seed choice experiments were similar in containing relatively little water (6.49–9.67%), but varied slightly more in their energy content (17.72–24.27 kJ/g) (Table 2).

Table 2. Energy density and water content (mean ± SD) of five seed species used in seed choice experiments with the sandy inland mouse (*Pseudomys hermannsburgensis*) in the Simpson Desert.

Seed	**Energy density kJ/g**	**Water (% ± SD)**
Triodia basedowii	17.72 ± 0.78	6.49 ± 1.81
Grevillea stenobotrya	24.27 ± 0.47	8.51 ± 1.94
Trachymene glaucifolia	19.76 ± 2.24	9.67 ± 2.49
Goodenia cycloptera	22.82 ± 0.60	6.74 ± 1.54
Eremophila macdonnellii	18.19 ± 0.36	7.95 ± 1.30

Seed choice.—Experiments to examine seed choice by *P. hermannsburgensis* were carried out on five separate occasions over five years. The results obtained on each occasion are presented separately.

In *November 2010* very little seed was taken on one night only (Fig. 1), precluding the possibility of any statistical analysis. GUDs were lower at dishes under the cover of spinifex (mean = 9.64 ± 4.46) than at dishes in open sand (mean = 16.3 ± 2.95) ($F_{1,19} = 15.97$, $P < 0.001$). Tracks of sand goannas (*Varanus gouldii*) were identified on the two sand transects over three days, and one feral cat was observed during spotlighting on a single occasion.

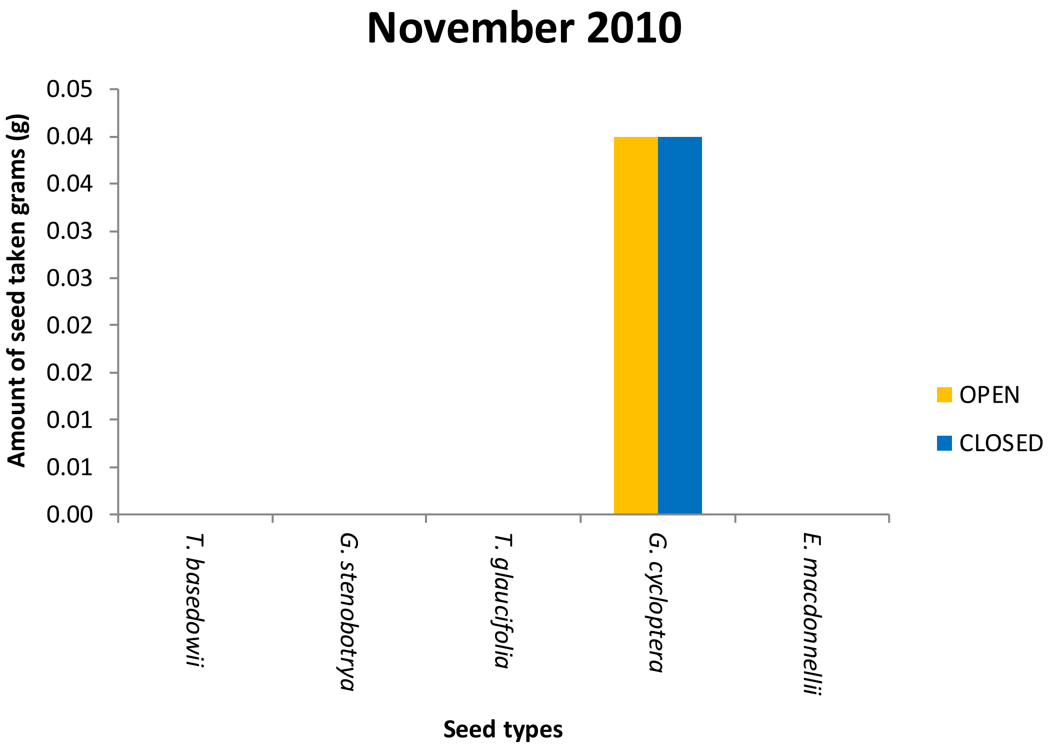

Figure 1. Quantity of seed removed from experimental seed dishes presenting five species of native seed by sandy inland mice (*Pseudomys hermannsburgensis*) over a period of five nights in the Simpson Desert, November 2010. One species of seed was taken on one night only.

In *May 2011* the five seed species were all sampled by *P. hermannsburgensis*, but different amounts of each species were removed (Fig. 2). More *E. macdonnellii* seed was removed from the open microhabitat than the closed in contrast to the pattern for the remaining seed species, resulting in a microhabitat × seed type interaction ($F_{4,70}$ = 2.70, P = 0.037). A strong main effect for seed species ($F_{4,70}$ = 4.91, P = 0.0015) arose from greater consumption of *T. basedowii* and *G. stenobotrya* than other species, and greater seed removal overall from under spinifex resulted in a microhabitat effect ($F_{1,70}$ = 4.12, P = 0.046).

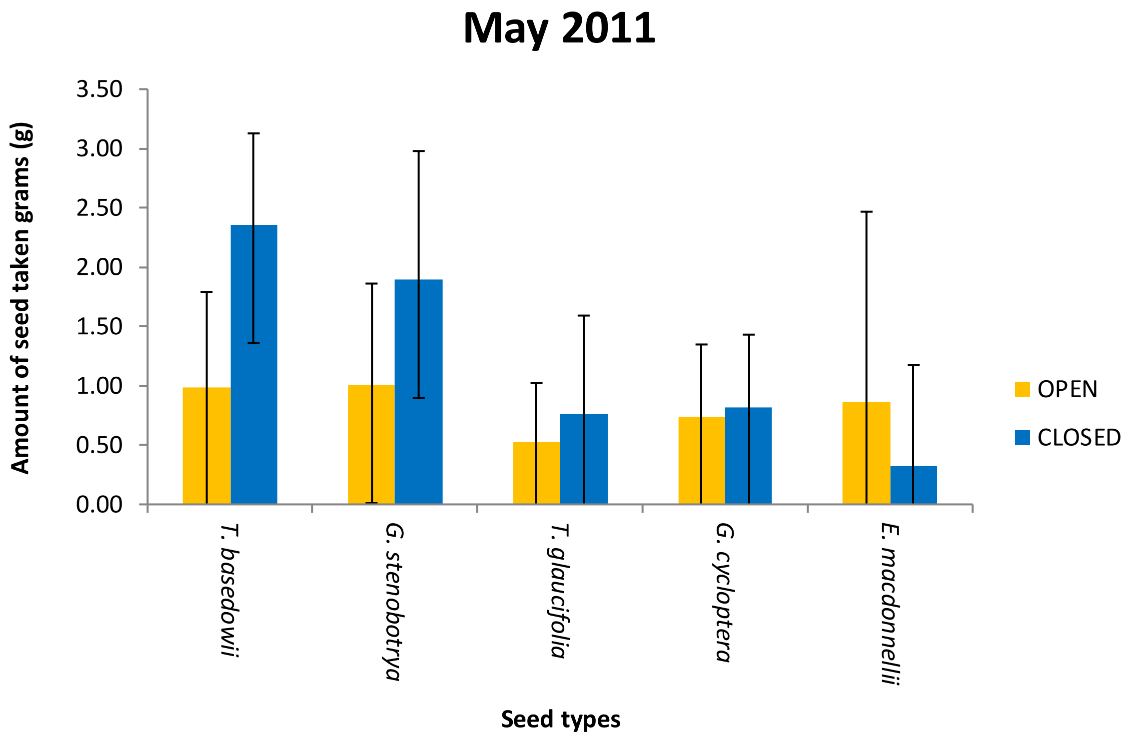

Figure 2. Quantity of seed removed (mean ± SD) per night from experimental seed dishes presenting five species of native seed by sandy inland mice (*Pseudomys hermannsburgensis*) averaged over a period of eight nights in the Simpson Desert, May 2011.

GUDs were again lower at dishes under the cover of spinifex (mean = 6.20 ± 4.89) than at dishes in open sand (mean = 13.20 ± 5.63) ($F_{1,18}$ = 8.80, P = 0.008).

This experiment was conducted when rodent numbers were high due to recent rains, but many of the plants had not produced seed and food was in short supply. Predator transects recorded the presence of fox, cat and dingo across three days at two of the four transect sites. Three cats were recorded during one night of spotlighting.

In *June 2014* (winter), natural food resources and rodent numbers were both low. Predators were present in low numbers, with evidence of prints and scats found within the study area. There was one confirmed fox and one dingo sighting, and two unconfirmed but possible cats or foxes recorded during two nights of spotlighting. One transect site recorded cat prints on the middle transect on two nights and fox prints on the swale transect once. GUDs, again, were lower at dishes under the cover of spinifex (mean = 6.0 ± 5.0) than at dishes in open sand (mean = 13.38 ± 4.41) ($F_{1,15}$ = 10.41, P = 0.006). The seed choice results here parallel those of May 2011, with a strong interaction ($F_{3,56}$ = 4.437, P = 0.007; ANOVA omitted *E. macdonnellii* as no seed was eaten) arising from the relatively greater consumption of one seed species, *T. glaucifolia*, in the open microhabitat compared with the closed, whereas other seeds tended to be eaten more under cover of spinifex (Fig. 3). There were also main effects of seed species ($F_{3,56}$ = 3.39, P = 0.024) and microhabitat ($F_{1,56}$ = 6.72, P = 0.012).

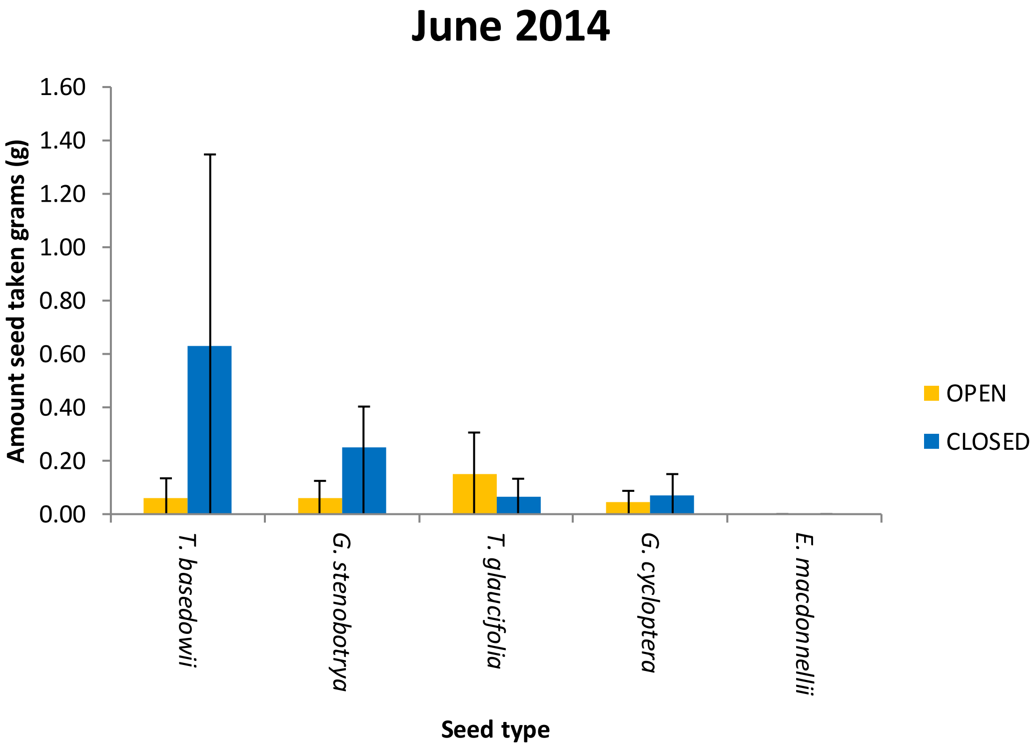

Figure 3. Quantity of seed removed (mean ± SD) per night from experimental seed dishes presenting five species of native seed by sandy inland mice (*Pseudomys hermannsburgensis*) averaged over a period of eight nights in the Simpson Desert, June 2014.

In *April 2015*, a dry period when natural food and rodent numbers were both low, there was little evidence of predator presence in the immediate study area with no prints or scats found during the trip on the prepared transects or even opportunistically on access tracks. No predators were observed during two nights of spotlighting. GUDs tended to be lower at dishes under the cover of spinifex (mean = 6.45 ± 2.25) than at dishes in open sand (mean =

8.2 ± 1.46) ($F_{1,19}$ = 4.342, P = 0.051). In the seed choice experiment (Fig. 4), open microhabitat was preferred ($F_{1,40}$ = 4.368, P = 0.043), as was *G. stenobotrya* among the seed species ($F_{3,40}$ = 39.25, $P < 0.001$), but there was also a strong interaction between microhabitat and seed type ($F_{3,40}$ = 7.404, $P < 0.001$). The ANOVA omitted *E. macdonnellii* as no seeds of this species were eaten.

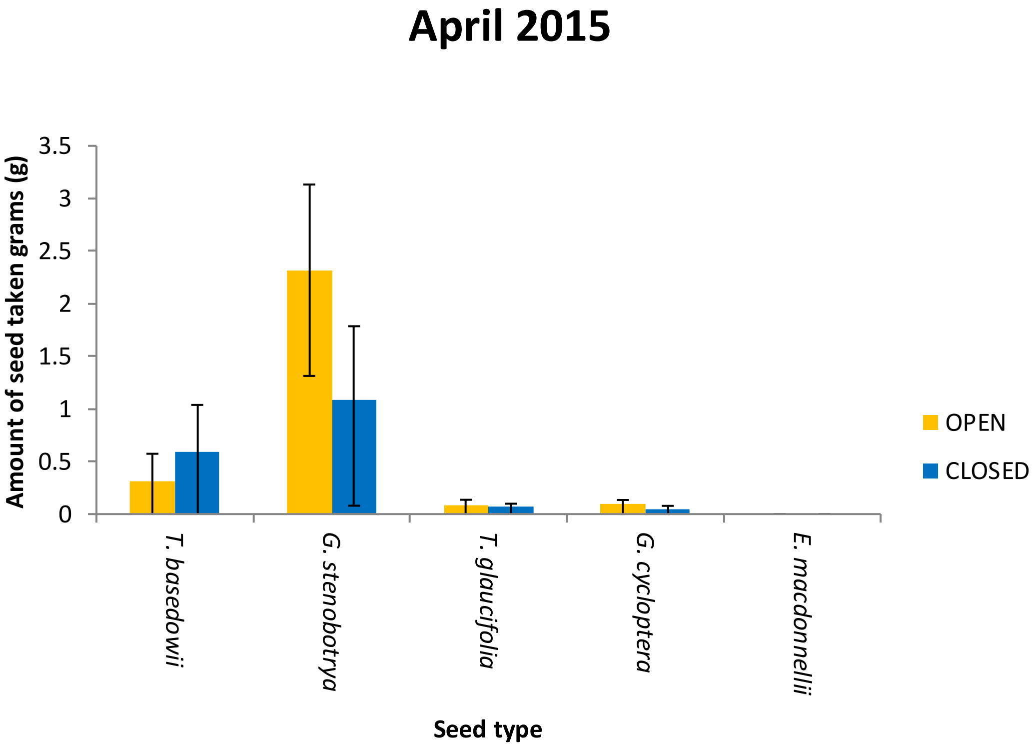

Figure 4. Quantity of seed removed (mean ± SD) per night from experimental seed dishes presenting five species of native seed by sandy inland mice (*Pseudomys hermannsburgensis*) averaged over a period of six nights in the Simpson Desert, April 2015.

In *June 2015*, a period when natural food and rodent numbers were both low owing to the continuing dry conditions, predator activity also remained low. There was little evidence of predator presence, with no prints or scats found within the study area on tracks or transects, and two foxes sighted by spotlighting on one night. GUD trials (using peanuts) could not be run in June 2015 for logistical reasons, but the cafeteria seed choice experiment was still conducted in June 2015 while the GUD trials (using peanuts) were completed three months later when conditions had little changed, in September 2015. GUDs were lower at dishes under the cover of spinifex (mean = 5.11 ± 2.42) than at dishes in open sand (mean = 7.67 ± 1.58) ($F_{1,16}$ = 7.03, P = 0.017). In the seed choice experiment, there was no interaction between seed type and microhabitat ($F_{3,40}$ = 1.255, P = 0.303) and no main effect of microhabitat ($F_{1,40}$ = 0.414, P = 0.524), but a strong effect of seed type ($F_{3,40}$ = 18.59, P < 0.001), with *G. stenobotrya* seed being consumed more than any other species (Fig. 5). As before, this ANOVA omitted *E. macdonnellii* as no seeds of this species were eaten.

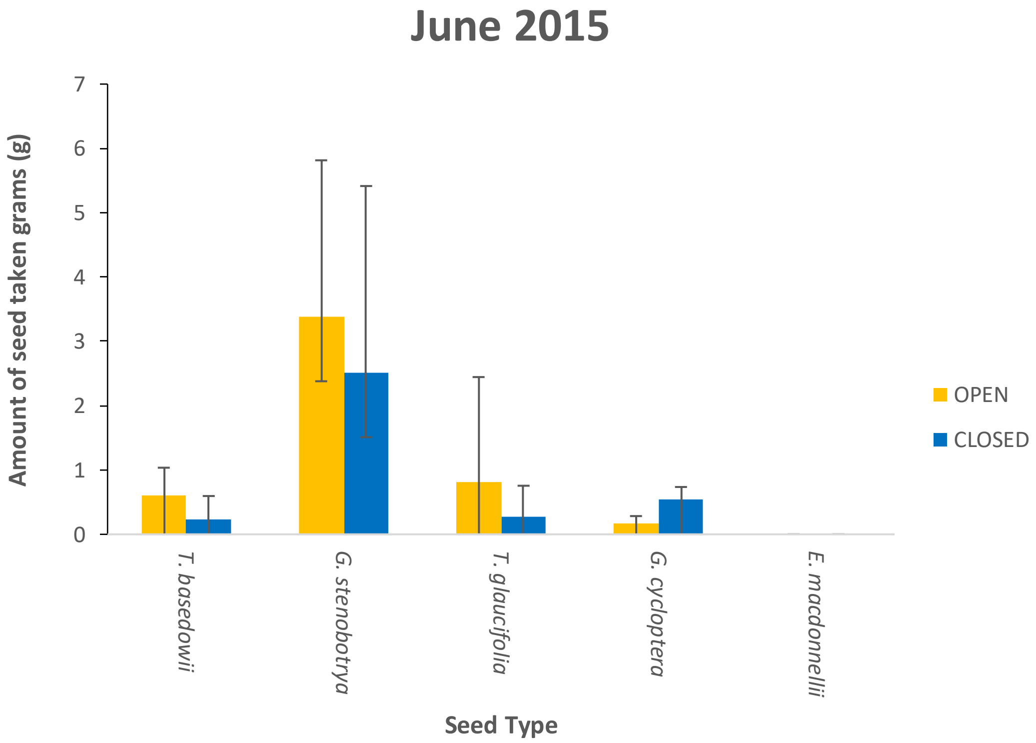

Figure 5. Quantity of seed removed (mean ± SD) per night from experimental seed dishes presenting five species of native seed by sandy inland mice (*Pseudomys hermannsburgensis*) averaged over a period of six nights in the Simpson Desert, June 2015.

Discussion

The results generally support the initial hypothesis and also the premises on which it was based. Thus, in support of the first prediction, the major predators of *P. hermannsburgensis*—the feral cat and red fox—were regionally present throughout the period of study and active locally at the experimental site on at least four of the five occasions when seed choice experiments were run. Both predators were more likely to attack potential prey in open compared with closed spinifex microhabitats, and *P. hermannsburgensis* perceived this difference in predation risk by spending less time foraging in the open (high GUDs) compared to under cover (low GUDs). In support of the second prediction, animals generally accepted inferior quality seeds while foraging in risky open patches but, with more time to be selective, consumed higher quality seeds while under the cover of spinifex. These results support the expectations of optimal foraging theory (Kotler & Brown, 1988). However, there were also some disparate and unexpected results that are contextualised further below.

Key premises in food choice experiments are that food types differ in quality and that these differences can be recognised and form the basis for food-type selection by foragers (Illius & Gordon, 1993; Manly *et al*., 2007). The decision to use the five chosen seed species in these experiments followed observations that all would have been familiar to *P. hermannsburgensis* (Chapter 3) and were also likely to differ in quality (Murray & Dickman, 1997). Thus, *T. basedowii* had the highest water content (39.2%) of 14 seed species assayed in this latter study, as well as a relatively high nitrogen content, whereas *G. stenobotrya* seeds had the highest energy content (Murray & Dickman, 1997). *Eremophila*, by contrast, had the lowest water content. The results of the present study also found that *G. stenobotrya* seeds had the highest energy density, but water content values differed little between the five selected seed species, in contrast to the results of Murray and Dickman (1997). The values determined in this study would have differed from those found by Murray and Dickman (1997) as seed energy, water content and chemical composition can change due to many factors such as prior storage conditions of the seeds, the location of where the seeds were sourced and the time of when the seeds were collected; seed of the same species can vary greatly depending on soil, rainfall and temperatures (Kameswara *et al*., 2017).

Nonetheless, it was felt reasonable to assume a rank preference of seeds for *P. hermannsburgensis* (most preferred = *T. basedowii* and *G. stenobotrya*; intermediate preference = *G. cycloptera* and *T. glaucifolia*; least preferred = *E. macdonnellii*) for several reasons in addition to their energy and water content. In the first instance, this rank ordering reflects the numbers of these seeds observed to be eaten by *P. hermannsburgensis* in the field (note that no *E. macdonnellii* seeds were observed to be eaten at all; Chapter 3), and also approximates the ease of handling of the seeds by mice. For example, animals readily held the small seeds of *T. basedowii* and the large but flat seeds of *G. stenobotrya* in their forepaws while consuming them, but would have had difficulty—and experienced low net energetic returns—in attempting to break through the hard, spherical seeds of *E. macdonnellii*. The seeds of *G. cycloptera* and *T. glaucifolia*, while flat and easy to handle like those of *G. stenobotrya*, are relatively small and thus would yield less energy per seed than for *G. stenobotrya*. Secondly, it is possible that the low and relatively invariant water content of the seeds measured here was an artefact of the seeds having been stored for too long in paper bags, and thus drying out, before their water contents were measured. This dehydration effect would have been especially marked for the smallest seeds, *T. basedowii* (~4 mg). As attempts were made to use fresh seeds in the field trials, especially the early trials which used seeds of *T. basedowii* collected in abundance during a mast seeding event in late 2010, differences in seed water content were likely to have been more pronounced than suggested by the results in Table 2.

Accepting that the experimental seeds differed in quality, the results provide considerable insight into factors, especially predation risk, that influence diet choice in *P. hermannsburgensis*. Except in November 2010 when very little seed was taken, presumably due to high abundance of seeds in the landscape from recent rains, *P. hermannsburgensis* sampled four or all five seed species from the experimental dishes on every occasion thereafter, including seed species ranked as intermediate or lower quality. This result may reflect “partial sampling” or “partial preference” whereby foragers accept small amounts of food types that may not maximise energetic returns but yield benefits not provided by preferred food types such as 'top-up' energy or particular nutrients (Gilliam, 1990). Sih (1993) and Stephens *et al*. (2007), among other authors, note that partial sampling occurs commonly in foragers. As suggested by Murray and Dickman (1997), partial sampling may also be important in allowing *P. hermannsburgensis* to help them determine seed preferences.

Notwithstanding the partial sampling of seeds, in the seed choice experiments from May 2011 onwards *P. hermannsburgensis* consumed more *T. basedowii* or *G. stenobotrya* than the other seed species and least of *E. macdonnellii*, with generally small amounts of *G.*

cycloptera and *T. glaucifolia*. Most seeds also were consumed under cover of spinifex rather than in the open. These results accord with expectations based on foraging theory, as noted above, and with the strong preference of *P. hermannsburgensis* for *T. basedowii* and *G. stenobotrya* as shown by Murray and Dickman (1997). Beyond this, the results generally support the prediction that the mice accepted inferior quality seeds while foraging in risky open patches, whereas higher quality seeds were eaten while under the cover of spinifex.

In May 2011, all five species of experimentally placed seeds were eaten, albeit in varying quantities, the only occasion when this occurred. Live-trapping of small mammals that was taking place at the same time showed that populations of *P. hermannsburgensis*, and other rodents, such as the spinifex hopping mouse (*Notomys alexis*), desert mouse (*Pseudomys desertor*), long-haired rat (*Rattus villosissimus*) and house mouse (*Mus musculus*) were at their highest levels in 20 years; perhaps elevating competition for food resources and ensuring that any food that was encountered would be eaten (Dickman *et al*., 2014; Greenville *et al*., 2016). In May 2011, in addition, an interaction between seed species and microhabitat arose because more *E. macdonnellii* seed was removed from the open than the closed microhabitat, whereas all other seeds—especially *T. basedowii* and *G. stenobotrya*—were consumed primarily under cover of spinifex. Predator activity was notably high at this time, suggesting that *P. hermannsburgensis* focussed foraging effort on the most profitable seeds in covered microhabitat patches where only occasional predator activity occurred, but accepted inferior quality seeds in the open microhabitat patches where the elevated probability of encountering a predator made it too risky to spend time there on seed selection. Similar results prevailed in June 2014, but here the seed × microhabitat interaction arose because of the relatively greater consumption of *T. glaucifolia* in open microhabitat patches than in the closed patches, in contrast to other seeds that were eaten largely in patches under the cover of spinifex.

Results in 2015 diverged from the patterns seen in earlier years. More *G. stenobotrya* seed was consumed than *T. basedowii* seed, and *P. hermannsburgensis* showed little preference for foraging under the cover of spinifex. The switch to preferencing *Grevillea* seeds may have resulted from the experimental seeds of *T. basedowii* having become drier and less nutritious over time than the larger seeds of *G. stenobotrya* (owing to prevailing bust conditions, all seeds used in the 2015 trials were 1–2 years old). In addition, animals may have been less familiar with the seeds of *T. basedowii* than of *G. stenobotrya* as spinifex seeds decline in the natural soil seed bank more quickly than those of most other plant species (Predavec, 1994; Ricci, 2003). One of the tenets of foraging theory is that animals should focus increasingly on profitable prey as their encounter rates with these prey increase, and drop those prey that are rare and less profitable (Stephens & Krebs, 1986; Sih, 1993). Seeds of *T. basedowii*, though still profitable, may thus have been eaten less by mice at the experimental seed dishes because of their increasing rarity in the soil seed bank, and dropped in favour of the more-familiar seeds of *G. stenobotrya*. Another potential reason for the switch is that more energy and time would have been required to process *T. basedowii* seeds as the outer parts of the seed (hull) would need to be removed to consume the seed, whereas the *Grevillea* seed requires little handling as the shell can be consumed. Drying of the *T. basedowii* seeds would have exacerbated the difficulty of removing the seed hulls and also required greater expenditure of salivary water to process the seed itself (Vander Wall, 1995).

In April 2015 more seed was taken from patches of open microhabitat, and in June 2015 there was no microhabitat effect at all. April 2015 was unusual in that no predators were detected on site and there was only weak evidence from the GUD results that mice perceived open microhabitats to be more risky than those under cover of spinifex. It can be conjectured that the lack of predators led to the different results in April 2015 compared to the previous results, with relatively more food being consumed in the open than in the closed. Presumably rodents perceived minimal risk in the open microhabitat patches as there would have been few or no cues to predator presence in the area. A similar explanation might apply to the results for June 2015, when predator activity was also very low.

In support of this latter interpretation, previous research has shown that when resources such as food are limited rodents will forage equally in closed and in risker open habitats (Kotler *et al*., 1998); Dickman *et al*. (2010) also found that during bust phases of the population cycle when predator numbers were low, *P. hermannsburgensis* returned similar GUDs in open and closed microhabitats. There is also some evidence that *P. hermannsburgensis* perceives reduced risk of predation when predator numbers are low during times of drought (Dickman *et al*., 2011). If animals perceived similar (low) risk of predation in both open and covered microhabitats, it is perhaps not surprising that the highly preferred seeds of *G. stenobotrya* were consumed in both microhabitats in greater amounts than the other seeds. Animals would have had more time to choose preferred seeds rather than quickly taking the first seeds encountered, as might be expected from theoretical considerations (Charnov, 1976; Perea *et al.*, 2011). Overall, the earlier results (2011–2014) provide good examples of prey switching, where animals switch to lower preference food items when the cost of moving to another patch is too high, as from the risk of predation; the later results (2015) show that once the risk of predation is low, rodents will spend more time foraging for preferred food types even in open sites and take the time to choose seeds rather than take any that happen to be encountered (Veech, 2001; Perea *et al.*, 2011).

In most previous studies of the effects of predation risk on diet choice, researchers have set up different predictions from those here. For example, Hay and Fuller (1981) predicted that heteromyid rodents would experience greater predation risk in open microhabitats and, in consequence, select high quality seeds while foraging there to justify exposing themselves to elevated predation risk. These predictions are appropriate for heteromyids but not for *P. hermannsburgensis*. Heteromyids generally, and the two species studied by Hay and Fuller (1981)—the pocket mouse *Perognathus fallax* and kangaroo rat *Dipodomys merriami*—can pick up and store seeds in cheek pouches before moving quickly to sheltered sites to consume them. Hence these animals benefit from being selective foragers in risky habitats. By contrast, no Australian desert rodents, including *P. hermannsburgensis*, have cheek pouches for temporary food storage (Breed & Ford, 2007). Seeds obtained in risky open habitats have to be eaten on the spot or, if a suitable size and shape, carried in the jaws to a sheltered site, providing less time and opportunity to be selective. In most other studies of predation risk on diet choice, both theoretical and empirical, dietary diversity has been predicted to decline under high predation risk because animals are forced to forage in safe microhabitats where the range of available prey is restricted and often suboptimal (Lima & Dill, 1990; Sih, 1993; Mukherjee & Heithaus, 2013; Rinehart & Hawlena, 2020). Such expectations were not appropriate in this study because both the range of prey types and amount of each prey type were deliberately held constant between microhabitat patches that were perceived as safe and risky by the study species. The results of the present work therefore appear to be novel and confirm that risk of predation can have significant and predictable effects on diet choice by foragers in the 'landscape of fear' (Laundré *et al.*, 2009, 2017).

In conclusion, the results of this study provide new insight into the influence of predation risk on microhabitat use and foraging habits of *P. hermannsburgensis*, especially with respect to the seeds that animals select to eat. The mice appear to be sensitive to predator presence and to the risk of predation, calibrating where they forage and what they consume according to the degree of risk they perceive. Other desert rodents are also sensitive to the risk of predation while foraging, and this sensitivity affects how much food they consume in different microhabitats (e.g., Kotler & Brown, 1988; Orrock *et al*., 2004; Bedoya-Perez *et al*., 2013; Laundré *et al*., 2017). Future research may reveal whether this sensitivity to predation risk also translates into selection of food types that vary in quality, as it does in *P. hermannsburgensis*. The results of this study help to explain the small amount of time that *P. hermannsburgensis* spend eating while active (< 1%) and the high levels of vigilance that they display (Chapter 3), but also hint at other factors that may influence diet choice. For example, the switch in the preference of mice for the seeds of *T. basedowii* to those of *G. stenobotrya* between 2011–2014 and 2015 was striking. This could have arisen from a decline in the quality (e.g., water content) of *T. basedowii* seeds, but could it also reflect a likely increase in the rarity of these seeds in the soil seed bank and hence a decline in the familiarity of mice with these seeds as a food source? Prey-type familiarity is an important component of optimal diet and foraging theory, and this topic is investigated further in Chapter 6, after an investigation into the effects of seed burial and seed moisture in the next chapter.

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Appendix 1

A pilot study was conducted to test whether the odour of domestic cats (*Felis catus*) could function as an effective and direct cue for foraging risk for the sandy inland mouse (*Pseudomys hermannsburgensis*) in giving-up density experiments and subsequent seed choice experiments. Previous research by Vyas *et al.* (2007) had indicated that the integumental odours of cats act as a foraging deterrent in small rodents and could be collected readily on cotton cloth towels. Although cat urine or faeces can provide effective cues to cat presence, it is difficult to collect and transport these materials in quantity to remote field sites for experimental purposes; hence cat body odour was used in pilot trials to determine its effectiveness in provoking an anti-predatory response in *P. hermannsburgensis*. Cotton towels were rubbed on domestic cats in Sydney for 5 minutes in a manner similar to the method used by Vyas *et al.* (2007). The towels were then placed in plastic zip-locked bags and kept refrigerated at -2–3 °C before being transported in a portable refrigerator to the experimental site.

To test the effectiveness of the cat odour on the towels, *P. hermannsburgensis* were captured near the study site during concurrent live-trapping as part of other studies (Dickman *et al*., 2014; Greenville *et al*., 2016), and mice were then placed singly into an 'interview chamber' and left overnight. Interview chambers were constructed using a 30-cm diameter bucket (which animals used as a nest box) connected by PVC pipes (30 cm long, 5 cm diameter) at the base of the bucket to three plastic storage bins (66 × 45 × 27 cm high), as described in detail by Bleicher and Dickman (2016). Animals are thus free to move along the pipes from the central bucket and visit any or all of the bins during the night. The bucket was equipped with a single egg carton to act as a nest box, and this and each storage bin were provided with a 1-cm layer of sand to provide a familiar substrate for experimental animals. Each storage bin was provided with a bowl containing food (10 quartered peanuts). One bin was then provided with a section (5 × 5 cm) of cat-scented towel placed near the food bowl, another with a section of clean towel (procedural control: clean towels were transported and contained in the same way as the cat-scented towels, but had had no contact with cats), and the third bin had no towel. The next morning, peanuts were counted in each storage bin to gauge how much time had been spent foraging by animals in each. After one night in an interview chamber, animals were released back at their site of capture on the previous day and were not used again. Newly-captured animals were used on the next night, with the storage chambers thoroughly cleaned and the order of presentation of towel treatments randomised between storage bins for each trial occasion. Interview chambers were set up on dry nights near the study site and were thus exposed to ambient temperature conditions.

Initial testing showed that all mice (*n* = 8) avoided storage bins with cat odour on the first night the cat-scented towels were used, and consumed food equally from the other storage bins. However, further testing indicated that the effects of the odour lasted only for the first night, and after this the mice (*n* = 8) did not differentiate between the bins and used them all equally. The results show that rubbing towels on cat fur will capture cat body odour; *P. hermannsburgensis,* at least, avoid this odour when it is relatively fresh, but perceive no threat after a single night. The time of use of scented towels is therefore limited, because the odour presumably dissipates or becomes ineffective after 24 hours. The scented towel approach thus may be useful for short periods of study, but not for giving-up density or seed choice experiments that run over several days as this would require large quantities of cat-rubbed towels and considerable labour to change the towels daily. Overall, it was concluded that the time-cost of preparing and continually deploying fresh towels and the logistic difficulties of transporting sufficient material and keeping it cool were too great to make this a viable methods for manipulating predation risk in the present study. Hence, indirect approaches to creating foraging patches of high vs low predation risk were explored using foraging patches in different microhabitats: open sand and under the cover of spinifex hummocks.

Chapter 5. Foraging and seed selection in rodents: influence of moisture and seed burial depth

Abstract

This study aimed to determine the effect of moisture and seed depth on the foraging habits of the sandy inland mouse (*Pseudomys hermannsburgensis*) in the sand dune environment of the Simpson Desert, central Australia. Groups of five *Grevillea stenobotrya* seeds, a preferred seed species for the mice, were placed on the surface of sand (0 cm) and at depths of 0.5 cm, 1.5 cm, 3.0 cm and 5.0 cm at seed-stations, and water was added daily to half the stations to provide an orthogonal seed depth × moisture treatment design. The results were surprising in that moisture did not significantly affect seed detection or consumption as had been predicted, and that mice were able to detect seeds buried in sand at 5 cm. As predicted, however, seed burial depth varied strongly and inversely with seed detection and consumption on the three occasions when experiments were repeated, with most seeds being consumed on the soil surface and at the shallow depth of 0.5 cm. The results from this research reveal more information about the foraging habits of *P. hermannsburgensis* and also suggest that it has acute and highly developed olfactory senses. It is suggested that a keen olfactory sense that allows *P. hermannsburgensis* to detect deeply buried seeds in dry sand represents a key survival adaptation that allows the species to persist in desert habitats; it is also an adaptation that appears not to have been reported in previous research on Australian desert rodents.

Introduction

The concept of optimal foraging predicts that animals should maximize fitness by finding food that maximizes their net energy gain per unit of feeding time (Stephens & Krebs, 1986). Numerous theoretical and empirical studies have sought to test and refine the basic concept, with examples drawn from a wide range of consumer organisms (e.g., Heth *et al*., 1989; Stephens *et al*., 2007; Calver & Loneragan, 2023). These studies have shown that many factors can interact to influence the decisions made by animals when foraging. In the first instance animals must be able to detect and locate food resources, and overcome challenges that may be imposed if those resources are cryptic, buried or otherwise hidden. Animals then must decide if the benefit of handling and consuming the food justifies the energy expenditure required to process it, as well as balance any associated risks such as being consumed by a predator (Krivan, 1996).

Many terrestrial mammals face the challenge of finding food resources that are buried below the surface of the ground. For some species, such as those that consume the roots of plants or the fruiting bodies of subterranean hypogeous fungi, the presence of host plants may provide above-ground visual cues that indicate to consumers where foraging is likely to be most successful (Hawker, 2008; Merritt, 2010; Elliott *et al*., 2022). Similarly, domestic cats (*Felis catus*) may use burrow holes as visual cues to the locations of below-ground prey species such as small mammals (Dickman & Newsome, 2015). For other species, sounds made by subterranean prey may allow foragers to detect them. The bat-eared fox (*Otocyon megalotis*), for instance, uses auditory cues to detect the faint scraping sounds of termites as they move along subterranean galleries (Renda & le Roux, 2017). The Namib Desert golden mole *Eremitalpa granti namibensis* similarly uses auditory cues to detect termites, but is guided to them indirectly by the low-frequency seismic sounds that are generated when wind blows through the leaves of isolated grass hummocks where the termites are localized (Narins *et al*., 1997, 2016). However, for many mammals that exploit buried prey, odour is a particularly important cue. Churchfield (1980) reported that common shrews (*Sorex araneus*) could use olfactory cues to detect and excavate blowfly (*Calliphora* sp.) pupae that had been buried at depths of ≥ 20 mm in soil, and Sörensen *et al*. (2019) showed that meerkats (*Suricata suricatta*) could detect and distinguish different buried foods and food odours in controlled tests in captivity.

In rodents that take seeds as part of their diet, olfaction is likely to be crucial in finding buried seeds as this food type can be neither seen nor heard. Animals could potentially use visual cues to direct their foraging, such as under shrubs or patches of leaf litter, but in many plant species strategies to ensure seed dispersal mean that such cues may not always be reliable. In arid environments, especially, wind and sand movement cause seeds to be mixed and buried in sand (Kotler *et al*., 1993) so there are no surface cues to seed presence; in these conditions many rodents have adopted the strategy of actively seeking seeds from the thin, uppermost layers of loose sand (Krasnov *et al*., 2000). Observations of foraging in the sandy inland mouse (*Pseudomys hermannsburgensis*) in Chapter 3 suggest that this species similarly makes only shallow excavations for buried seeds.

The probability of rodents finding and retrieving seeds generally decreases as the depth of seed burial increases (Johnson & Jorgensen, 1981; Reichman, 1981; but see Taraborelli *et al.*, 2009). This is probably because odour cues from deeply-buried seeds will be attenuated compared with those near the surface, and would also require more energy expenditure to excavate once detected. In addition, making deep excavations is likely to increase animals' risk of predation as they cannot maintain vigilance when their heads are facing downwards in the soil, thus ensuring that the risks associated with deep digging will often outweigh the benefits of any food reward. Olfactory detection of buried seeds may be affected also by several other factors. For example, the depth and hardness of soil, the quality and quantity of seeds, and seed moisture content are important for some scatter-hoarding and other rodents (Geluso, 2005; Tull & Sears, 2007), while soil moisture is believed generally to influence animals' abilities to detect buried seeds (Frank, 1988; Vander Wall *et al.*, 2003). Most seeds are hygroscopic and rapidly absorb any available moisture, which triggers the release of odorants by release of organic solutes and odorous volatile molecules, which in turn make seeds easier for rodents to detect (Vander Wall, 1998; Vander Wall *et al.*, 2003; Taraborelli *et al.*, 2009). Murray and Dickman (1994a,b) found that the natural moisture content of seeds was a contributing factor in seed selection and consumption by *P. hermannsburgensis*.

Numerous dietary studies on rodents in the world's deserts, particularly in the south-west of North America, confirm that seeds are consumed by many species (Kelt, 2011). The diets of several species of native Australian desert rodents have also been shown to contain seeds (Murray *et al*., 1999) but, in contrast to the wealth of research in the Americas, the foraging habits and factors influencing the diets of Australian desert rodents have been little studied (Murray & Dickman, 1994a; Kelt, 2011). There is little evidence that Australian desert rodents cache seeds (Breed & Ford, 2007; Jackson *et al*., 2023; *cf*. Baker *et al*., 1993), and thus memory is likely to be less important in seed detection in Australia's murids than in heteromyid, sciurid and other rodents elsewhere in the world where landmarks and spatial memory are used to find buried seeds (Lavenex *et al*., 1998; Yi *et al*., 2021). Using the sandy inland mouse (*Pseudomys hermannsburgensis*) as a focal species, the objective of the present study was to determine to what depth foraging animals can detect buried seeds and the effect of adding moisture to buried seeds. Using seeds of an energetically profitable and preferred species, *Grevillea stenobotrya* (Chapters 3 and 4), I hypothesized that: 1) there would be an inverse relationship between seed burial depth and the retrieval and consumption of the seeds by *P. hermannsburgensis*, and 2) retrieval and consumption of moist seeds would be greater than that of dry seeds. As in the previous chapter, these predictions were tested by field experiments carried out under natural conditions on free-living animals.

Methods

Study site

Research was conducted on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E). The landscape has long parallel sand dunes up to 8 m high and 0.5-1 km apart with hard claypans forming between the dunes. The dominant vegetation is hard spinifex (*Triodia basedowii*) with perennial shrubs such as *Acacia* spp., *Crotalaria* spp. and *Grevillea* spp. dominating on the dune crests; in the swales there are stands of trees such as mulga (*Acacia aneura*) and Georgina gidgee (*Acacia georginae*), as described in Wardle *et al*. (2015) and Chapter 2.

The climate of the Simpson Desert is highly variable, oscillating between prolonged dry ‘bust’ periods and brief but highly productive ‘boom’ periods that follow summer rains (Dickman *et al.*, 2010; Greenville *et al*., 2013). Over 94 years an average 199 mm/year of rain was measured at Marion Downs (a station located 120 km from Ethabuka). When the present study was carried out (2016 and 2017), rainfall was above average in 2016 (370 mm) but average in 2017 (205 mm); rainfall data obtained from a weather station next to the study site (Environdata, Warwick, Qld). Temperature varies with season: average daily temperatures are > 40°C in summer and often < 5°C in winter (Greenville & Dickman, 2005).

Study species

The study focuses on foraging of the sandy inland mouse (*Pseudomys hermannsburgensis*), a small (12 g), nocturnal native Australian rodent with a wide distribution in arid Australia. Most foraging occurs near sheltered microhabitats such as hummocks of spinifex and, in the Simpson Desert, activity is focused on the sides and in the swales of dunes (Predavec, 1994, 1997). The species' biology has been described in more detail in previous chapters.

The seed chosen for the experiments was collected from *Grevillea stenobotrya*. This shrub is native to, and common in, the study area and is a preferred seed type for *P.*

hermannsburgensis (Murray and Dickman, 1997; Chapters 3 and 4). Importantly too, for the experiments reported here, the large size of the seed means that it is easy for researchers to find in the sand once buried, and it can be collected in abundance after large rainfall events—such as those in 2016—have stimulated flowering and subsequent seed production.

Experimental protocol

Seed-stations were established within a dune-swale system that was known from nearby live-trapping studies to be a site of activity for *P. hermannsburgensis* (Greenville *et al*., 2016). The swale was used to increase the likelihood of visits from *P. hermannsburgensis* rather than other species such as the spinifex hopping-mouse (*Notomys alexis*) which were active mainly on and near the crests of sand dunes. To encourage seed consumption and reduce the fear of predation, seed-stations were placed close to hummocks of spinifex; previous research has shown that desert rodents often prefer to forage near shrubs that offer protection from predators (Thompson, 1982; Kotler *et al*., 1994), and Chapter 4 confirmed that spinifex hummocks markedly reduced the predation risk perceived by *P. hermannsburgensis*. Seed-stations were set at least 20 m apart.

To test the first prediction, five *Grevillea stenobotrya* seeds were placed at each seed-station either on the surface of sand (0 cm) or buried at depths of 0.5 cm, 1.5 cm, 3.0 cm or 5.0 cm, with $n = 20$ per treatment and allocation to treatment being made at random. The locations of seed-stations were marked using flagging tape. However, to facilitate later location of the precise site of seed placement or burial, especially if most or all seeds were removed, the five seeds were placed on top of a small square (2.5 × 2.5 cm) of aluminium flywire mesh. When covered with sand the mesh was invisible to foraging *P. hermannsburgensis*, and also allowed free drainage of water. Five seeds were used at each seed-station to increase the likelihood that they would be detected by *P. hermannsburgensis*, and because seeds of *G. stenobotrya* are often found naturally in small clusters of 3–7 seeds in the soil seed bank, presumably representing seeds that have fallen out of single seed pods. To test the second prediction, half the seed-station sites were allocated randomly to a moisture treatment such that $n = 10$ for each depth × moisture treatment. Seeds were moistened with ~50 mL of water each day using a 50 mL syringe barrel to apply water directly to the surface seeds and down to the appropriate depth for the buried seeds.

Seeds were set out at the seed-stations and water applied in the moisture treatments in the afternoons to allow time for water to be imbibed by the seeds and reduce any disturbance before mice were expected to become active after nightfall. The sand in a radius of ~12 cm around each station was swept and smoothed to capture the footprints of visiting small mammals and confirm their identity. The footprints of *P. hermannsburgensis* were confirmed using Moseby *et al*. (2009) and reference photographs made upon release of *P. hermannsburgensis* and other species of small mammals captured at the study site (Dickman *et al*., 2010). Each seed-station was checked in the early morning for seven consecutive days. Animal activity was recorded and seeds were counted; any seeds that had been consumed or removed were replenished, and footprints of the visitors were identified. The experiment was repeated three times, in June 2016, September 2016 and April 2017, with conditions on each occasion being dry.

Previous research has shown that some rodents are attracted by fresh disturbed soil alone (Thompson, 1982). To confirm that rodents in the present study were responding to the added seeds and not to other factors associated with the experimental protocol, such as the appearance or scent of freshly disturbed sand, 20 control sites were established; at 10 of these sites sand was freshly disturbed and at the other 10 sites sand was disturbed and ~50 mL water was added each day. These disturbances simulated those that were necessary to place and bury the seeds in the actual experiments. Sand was smoothed within a ~12 cm radius of each control site, and all sites were checked each morning for the seven-night duration of the experiment. The control sites were dispersed at random locations within the area of the actual experimental sites at distances of at least 20 m from the experimental seed-stations.

Statistical Analysis

As the variable of interest was the number of seeds removed by *P. hermannsburgensis*, results were screened to remove data from seed-stations with footprints indicating visits by non-target species. The numbers of seeds taken by *P. hermannsburgensis* were averaged per seed-station over the seven nights that each trial was run, and then compared between burial depth and moisture treatment using 2-factor analyses of variance (ANOVAs). Levene's test was employed to check for equality of variances (Quinn & Keough, 2002), with significance accepted when $\alpha \leq 0.05$. To visualize the overall dataset, scatter plots were constructed to show the spread of individual seed-station results, and further tests were carried out on the overall dataset to compare the separate effects of seed burial depth and moisture using a Wilcoxon rank sum test (dry vs wet treatments) and Kruskal-Wallis test (seed depth treatment) in R version 4.2.2 (R Development Core Team, 2018). Results from the control sites (with no seeds) were not included in tests with the experimental results as no or very few visits were recorded on any occasion.

Results

The control sites, with no added seeds, were scarcely visited by *P. hermannsburgensis*. Footprints were often recorded where animals had walked past or over the disturbed-sand control sites, but only two sites out of twenty controls over the three experiments conducted showed any sign of animals scratching at the sand surface and it was only a single occurrence at the site that was not repeated.

The lack of activity at control sites contrasted strongly with high levels of activity at the experimental sites where either surficial or buried seeds were available (Fig. 1). In June 2016 most seeds were removed from the soil surface, with significant ($F_{4,60} = 18.25$, $P < 0.001$) and monotonic declines in seed-take recorded at increasing burial depths. More seeds were taken in dry than in wet sand ($F_{1,60} = 6.823$, $P = 0.011$), and there was no burial depth × moisture interaction ($F_{4,60} = 0.785$, $P = 0.540$). Similar results were obtained in September 2016 (burial depth: $F_{4,60} = 138.7$, $P < 0.001$; moisture: $F_{1,60} = 0.639$, $P = 0.427$, but a relative increase in seed removal with depth in dry soil resulted in an interaction: $F_{4,60} = 18.27$, $P < 0.001$) and in April 2017 (burial depth: $F_{4,60} = 147.5$, $P < 0.001$; moisture: $F_{1,60} = 0.333$, $P = 0.566$); an interaction ($F_{4,60} = 2.914$, $P = 0.029$) arose from more seeds being removed from wet soil on the surface and at 0.5 cm deep, whereas more seeds were taken from dry sand at depths of 3.0 and 5.0 cm (Fig. 1).

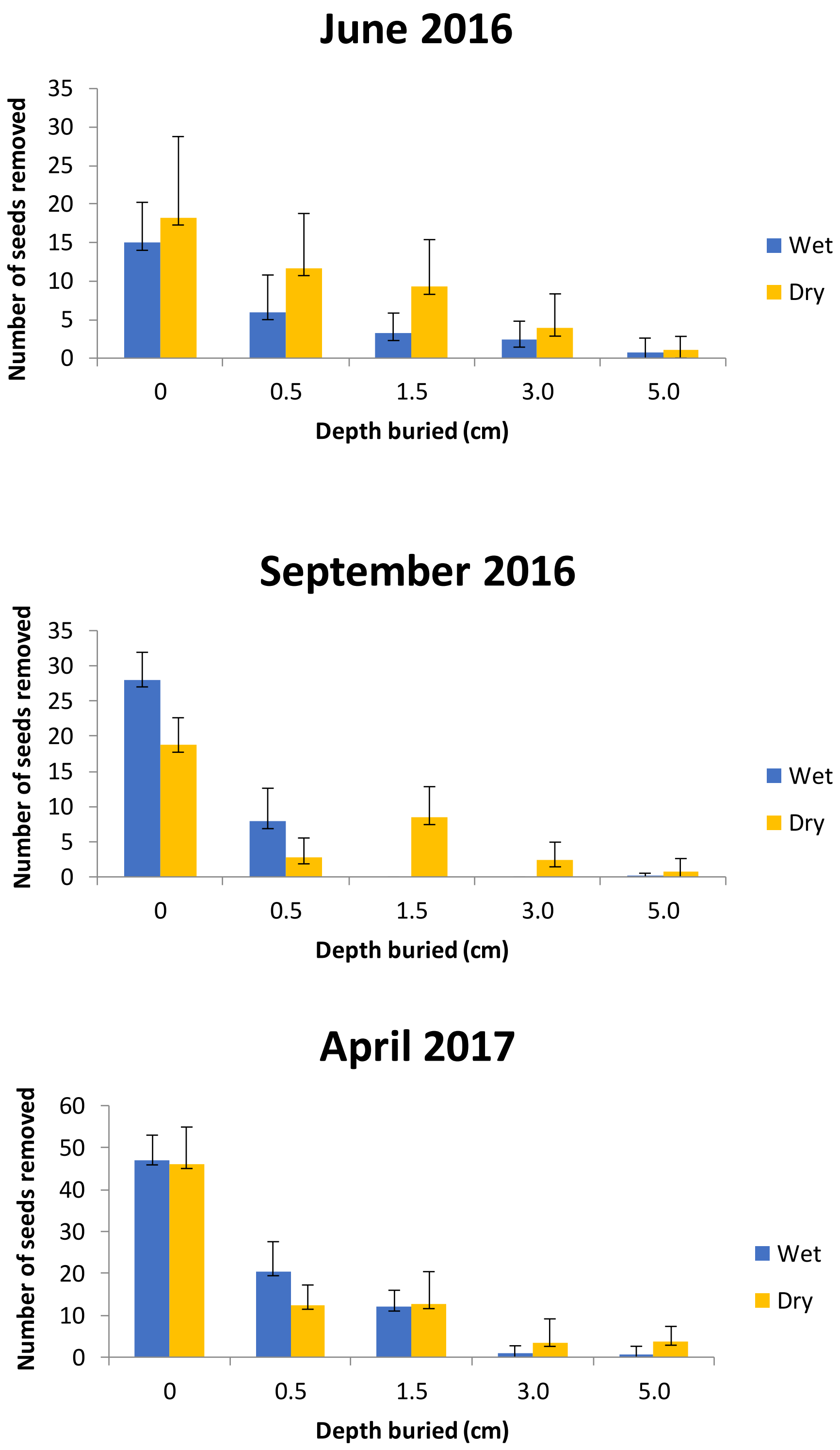

Figure 1. Number of seeds of *Grevillea stenobotrya* removed (means ± SD) per night by sandy inland mice (*Pseudomys hermannsburgensis*) at different soil depths (0, 0.5, 1.5, 3.0 and 5.0 cm) on three occasions and under either dry or wet soil conditions in the Simpson Desert.

Over the entire dataset (Fig. 2) depth had a highly significant effect on seed removal (H_4 = 538.85, $P < 0.001$), but there was no effect of adding water ($w = 554884$, $P = 0.7143$).

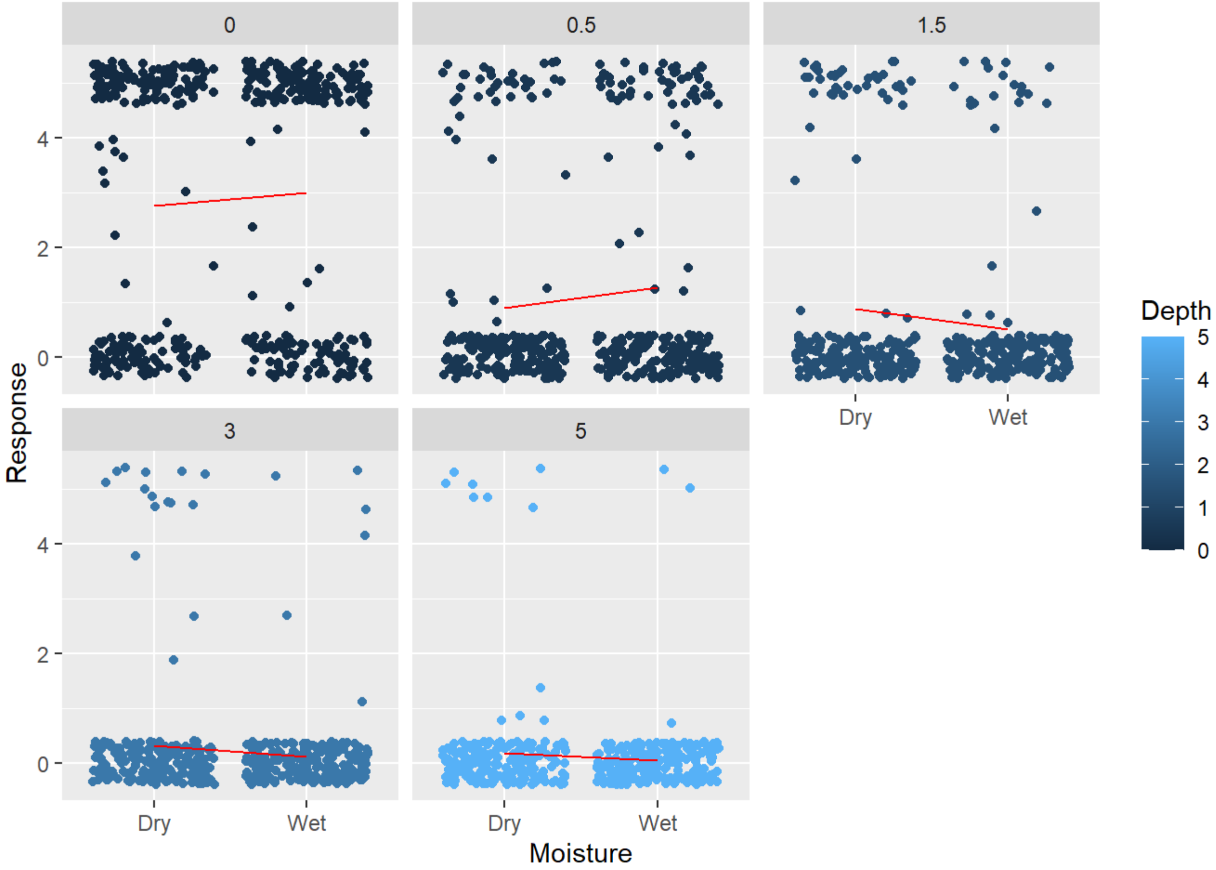

Figure 2. Scatter plot showing numbers of *Grevillea stenobotrya* seeds removed (response) by sandy inland mice (*Pseudomys hermannsburgensis*) at different soil depths (0, 0.5, 1.5, 3.0 and 5.0 cm) and under either dry or wet soil conditions pooled from three field experimental occasions in 2016 and 2017 in the Simpson Desert. Red lines show overall means. Note the 'all or nothing' pattern of seed-take, with either no seeds or all five seeds removed under most treatment conditions.

Although it was not part of the initial hypothesis testing protocol, observations suggested that more seeds were consumed each day of the 7-day trials. An *ad hoc* Kruskal-Wallis test confirmed that this trend was significant (H_6 = 93.23, P <0.001).

Discussion

The results provide strong support for the first hypothesis that seed burial depth would vary inversely with the retrieval and consumption of seeds by *P. hermannsburgensis*, but no support for the second hypothesis that moist seeds would be preferred. The results showed clearly that mice mostly removed seeds from the surface or at shallow depths of 0.5 cm, and the deeper that seeds were buried the less likely they would be to be removed. I assume that 'removal' equates to 'consumption'. Although animals were not observed directly to eat the seeds in this experiment, *P. hermannsburgensis* is not known to cache seeds and are more likely to consume seeds where they encounter them, or to move only a short distance to eat under cover (Chapter 3). Residues of *G. stenobotrya* seeds were found occasionally at or near seed-stations, providing additional (albeit anecdotal) evidence that removed seeds were indeed consumed. As *P. hermannsburgensis* did occasionally consume seeds excavated from depths of 3.0 cm and 5.0 cm this illustrates that they can detect more deeply buried seeds, but the significantly low seed retrieval from such depths (Figs 1-2) indicates that the reward of food does not outweigh the energy and time expenditure and the likely increase in risk of predation. Several other studies have shown that rodents generally consume fewer seeds that are buried at increasing depths in leaf litter such as prairie rodents like the white-footed mouse (*Peromyscus leucopus*) and the deer mouse (*Peromyscus maniculatus*) (Clark *et al*., 1991) or western harvest mouse (*Reithrodontomys megalotis*) and the deer mouse (*P. maniculatus*) in desert soil (Johnson & Jorgensen, 1981). However, rodents sometimes detect and consume seeds equally from the soil surface and below the surface (e.g., Taraborelli *et al*., 2009), and in these cases it may be assumed that there is a positive reward: cost ratio. This could arise if rodents detect a large cache of buried seeds and / or are able to consume them or remove them quickly via storage in cheek pouches (Geluso, 2005).

Rodents often differ in their approach to foraging for seeds, with some species seeking large clumps of seeds and remaining at the clumps until the seeds are exhausted, and other species taking individual seeds from scattered locations, spending minimal time at any one location and consistently moving and seeking different food resources. Examples of these two foraging strategies have been observed in three desert rodent species: *Dipodomys deserti* and *Dipodomys merriami* utilize the first method of staying put and exhausting a food patch, while *Perognathus longimembris* forages by moving more frequently and selecting only certain seeds (Bowers, 1982; Thompson, 1982; Abramsky, 1983). There are benefits and risks with both foraging strategies. By remaining and exhausting one food patch less energy is used in moving and searching, and food is guaranteed. However, staying in one place increases predation risk as more time is spent away from shelter, and a premium is then placed on feeding quickly. By consistently moving and searching for new food patches predation risk may be lowered and animals should encounter a greater diversity of food types. However, energy expenditure is increased by continual searching and moving, and there is an increased risk of not encountering food or finding only food types of lower quality in other locations. The two foraging strategies appear to vary with species biology, with sedentary foragers more likely to have cheek pouches or caching abilities and bipedal locomotion for fast escape, and mobile foragers having no food storage abilities and quadrupedal locomotion (Randall, 1993; Spencer *et al*., 2014; Arregoitia *et al*., 2017).

Fig. 2 suggests that *P. hermannsburgensis* are more likely to stay and exhaust a food source once it has been found, rather than taking a small number of seeds and moving quickly to find different food resources. Thus, the mice mostly consumed all five seeds if they encountered them, irrespective of the depth at which the seeds were buried. Although this might appear to be counter-intuitive, as *P. hermannsburgensis* lack cheek pouches for quick seed removal and move quadrupedally, in Chapter 4 I showed that *P. hermannsburgensis* forage more intensively when under cover of spinifex, often exhausting the preferred seeds of *Grevillea stenobotrya*. Placement of the seed-stations near spinifex in the present study, and the use of *G. stenobotrya* seed, are therefore likely to have contributed to the complete seed-take when seeds were found.

Adding water to the experimental seeds did not increase seed detection or consumption by *P. hermannsburgensis*, in contrast to my initial expectations and to the results of comparative studies on rodents in other world deserts (Johnson & Jorgensen, 1981; Vander Wall, 1993; Taraborelli *et al*., 2009). Various reasons can be proposed to account for my results. Firstly, it may be that, even though seeds were replenished with water daily, 50 mL was insufficient to moisten the seeds. Water may have evaporated quickly from the sand surface or drained and dispersed away in the very dry desert sand. However, this seems unlikely as it was noted that seeds buried at depths of 3–5 cm, and sometimes more shallowly, were surrounded by wet sand when investigated. Perhaps future trials could soak the seeds for several hours and replenish the soaked seeds daily; Vander Wall (1993) found that seeds of antelope bitterbrush (*Purshia tridentata*) became sufficiently hydrated to be detectable by rodents after only 15 min soaking, but this is likely to vary between both seed and rodent species. Secondly, increased moisture may not have increased detection/consumption for buried seeds because the wet sand became more compacted, denser and heavier (Luo *et al*., 2014), therefore requiring more energy expenditure for mice to access the seeds. Thirdly, moisture may have made no difference to the odours of the *Grevillea* seeds, although further testing is required to confirm this. Finally, if the added water failed to hydrate the seeds, *P. hermannsburgensis* would have derived no hygric advantage in excavating them, using as much salivary and metabolic water to do so as for dry seeds (see Vander Wall, 1995 for discussion).

It has been suggested that some species of rodents, particularly desert heteromyids, have evolved very acute olfactory sensitivity, allowing them to detect buried seeds even under the driest conditions (Vander Wall, 1998). The results of the present study provide evidence that *P. hermannsburgensis* also has developed specialized olfactory abilities. *Pseudomys hermannsburgensis* is nocturnal and therefore must rely more on olfactory cues than visual cues to detect food; and the olfactory ability of the species is such that it can detect seeds regardless of the presence of moisture up to depths of at least 5 cm in sand, even if it excavates to such depths only infrequently. As noted by Vander Wall *et al.* (2003), such acute olfactory sensitivity should increase survival prospects and individual fitness in dry desert environments where water is often limited and seed resources may be buried at varying depths anywhere under the soil surface.

Although not tested formally as one of the study's predictions, it was noted that seed consumption from seed-stations increased the longer the experiment was run. This could be the result of rodents being initially fearful of human disturbance, such as odours, at the seed-stations, but becoming more familiar with the disturbance over time. I also noted that once a site was visited, it would often be revisited consecutively each night the experiment ran, irrespective of seed burial depth or moisture. This may suggest that the same individual mice were remembering and revisiting seed-stations at which they had successfully found food the night before, even though all five seeds usually were eaten on each visit. To test whether familiarity with a productive foraging site prompted return visits by mice I carried out a preliminary pilot trial. After the conclusion of the main seed-station experiments, I selected a single station (5 cm seed burial depth, no added water) at which all five *G. stenobotrya* seeds had been consumed each night. I buried five *G. stenobotrya* seeds in a new site just 5 cm away, and observed activity the following mornings. This showed that the original burial spot continued to be dug to 5 cm deep even though no seed was present, but the new burial site was also excavated with all five seeds consumed. Due to time restraints and the availability of seeds this trial was not repeated, but the results provided a hint that mice may return to the near vicinity of a productive site and focus their foraging there. Memory of profitable foods and productive sites, such as food caches, is an important component of seed foraging in some dry environments (Vander Wall, 1998). Memory-based experiments would be of value to determine if memory, as well as olfaction, influences food choice and foraging sites in *P. hermannsburgensis*.

In conclusion, this research has revealed that *P. hermannsburgensis* can detect and excavate seeds buried up to 5 cm deep in sandy soil, but preferentially take seeds on the soil surface or near-surface. This preference for surface seeds has the benefits of needing less energy expenditure to locate the seeds and of reducing the risk of predation as less time is required to be spent foraging. The lack of activity of mice at control sites where soil had been disturbed but not provided with seeds confirms that *P. hermannsburgensis* is not attracted to soil disturbance *per se*, and could not have used this as a sole cue to where to dig for seeds. Instead, the species almost certainly uses olfaction to detect buried seeds. Surprisingly, despite a wealth of research on desert rodents elsewhere indicating that moisture plays a role in seed detection and consumption, I found no evidence that adding water to preferred seeds of the study species increased either the detectability or consumption of those seeds. I speculate that *P. hermannsburgensis* has evolved acute olfactory detection skills that constitute a key adaptation for the desert environment where long, dry spells are frequent and being able to detect buried seeds is imperative for survival. The importance of this adaptation does not appear to have been appreciated in previous research on Australian desert rodents. There were also hints from the results that *P. hermannsburgensis* remembered productive foraging sites for its favoured seeds and returned to these increasingly frequently. The influence of seed familiarity is explored further in the next chapter.

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Chapter 6. Foraging and seed selection in rodents: effects of seed familiarity

Abstract

Other factors being equal, foraging theory predicts that animals should select common, familiar food types compared to rare ones because they will encounter these food types frequently and should therefore be able to recognize and handle them with speed and efficiency. This prediction was tested using the sandy inland mouse (*Pseudomys hermannsburgensis*), a small rodent endemic to arid and semi-arid environments in Australia. Although omnivorous, seeds comprise a large component of the diet of this species. I predicted that foraging mice should: 1) select seed species in correspondence with their likelihood of encountering them while foraging, and 2) differ in their choice of seed species between disparate sites. Two sites were established with disparate seed banks, and *P. hermannsburgensis* were provided with three seed species that were common in each site and three that occurred rarely in cafeteria-style selection experiments. In initial trials in 2016 mice consumed more common seeds than rare seeds in each site, in accordance with predictions. In subsequent trials in 2017, however, no seed-familiarity effect was detected and mice instead consumed the same two seed species (*Acacia dictyophleba* and *Grevillea stenobotrya*) in each site irrespective of their abundance in the seed bank. This result provided no support for my second prediction. Overall, the results suggest that familiarity influences seed selection at some times, or in certain places, but that other factors such as seed quality (energy, nutrient, water content) can override the familiarity effect. It is speculated that familiar seeds are taken to minimise the time spent foraging when environmental conditions are not limiting, but when *per capita* food or water resources are constrained animals are then more likely to focus their foraging on food types that minimise the risk of starvation. Further field experiments are needed to test these possibilities.

Introduction

Studies of desert rodents have been important in building our understanding of many aspects of population and community ecology, from elucidating the intrinsic and extrinsic factors that influence species' population sizes, dynamics and reproduction (Perrin & Boyer, 2000; Brown & Ernest, 2002; Barros *et al*., 2018; Berris *et al*., 2020) to the forces that shape the assembly of species communities (Kotler & Brown, 1988; Letnic & Dickman, 2010; Shenbrot, 2014). Much attention also has focused on uncovering the physiology and behaviour of desert rodents, with a great deal of behavioural research aimed at understanding the diets of desert rodents and the factors that influence their diets (Giannoni *et al*., 2005; Taraborelli *et al*., 2009; Vander Wall, 2010; Lasgaa *et al*., 2021). Because of the preponderance of research on granivorous heteromyid rodents in North America, a prevalent view is that heteromyids represent the 'norm' and that desert rodents generally converge in their biology on the heteromyid standard (e.g., Mares, 1980, 1993). Seeds do indeed form a substantial part of the diet of many desert rodents outside North America, such as in South America, South Africa, the Middle East and Asia (Prakash, 1994; Qumsiyeh, 1996; Marone *et al*., 2000; Seely & Pallett, 2008), and some rodents also have anatomical specialisations such as cheek pouches or bipedal locomotion, and behavioural traits such as seed caching, that accord with the heteromyid model (e.g., Randall, 1993; Degen, 2012; Arregoitia *et al*., 2017).

In Australia, several studies suggest that desert rodents are not highly convergent to desert rodents elsewhere. Dietary information indicates that most Australian desert species eat seeds as part of a more broadly omnivorous diet (Finlayson, 1941; Morton, 1979; Watts & Aslin, 1981; Murray & Dickman, 1994a,b; Murray *et al*., 1999; Ricci, 2003). No species have expansive cheek pouches such as those seen in heteromyids, and none is known to cache seeds (except for a single report that spinifex hopping-mice *Notomys alexis* store food during drought: Baker *et al*., 1993) (Predavec, 1994, 1997; Breed & Ford, 2007; Dickman *et al*., 2010, 2011). Despite these disparities, it is reasonable to expect that, when foods such as seeds are eaten, they will be sought and selected if they return a net profit to the forager (e.g., by maximizing energy intake per unit time while foraging) in accordance with the predictions of foraging theory (Kelrick *et al*., 1986; Sih & Christensen, 2001).

Many factors affect the foods eaten by granivorous and omnivorous rodents, such as the detectability of different food types, the ease of access to preferred food types, the energy and nutritional values of food, and external constraints such as the risk of predation or competition within and between forager species (Sih, 1993; Stephens *et al*., 2007). In Chapter 4 a further factor potentially influencing diet choice was postulated for the sandy inland mouse (*Pseudomys hermannsburgensis*): seed familiarity. The assumption that foragers should prefer familiar food types over foreign/exotic food types is based on the idea that familiar foods not only meet the energetic and nutritional requirements of foragers, but also can be found, recognized and consumed quickly and profitably simply because they are well known (Hughes, 1993; Greenberg & Mettke-Hoffmann, 2001). Rare or exotic food types, by contrast, may not be readily recognized and will often be approached with caution due to uncertainty on the part of the forager about whether it may encounter anti-predator defences (Partridge, 1981; Hughes, 1993; Visalberghi & Addessi, 2007). In most foragers recognition of familiar food occurs as a result of learning, and may be reinforced by the activation of endocrine signals when familiar food is encountered (Brown & Aggleton, 2001; Song *et al.*, 2013). In some foragers the tendency to persist with eating familiar food can even have negative fitness consequences if it means that more profitable alternative, but unfamiliar, foods are rejected (Costa *et al.*, 2016).

In rodents, many studies of food familiarity have focused on the question of how to induce pest species to eat unfamiliar foods such as baits that contain toxins, reproductive suppressant chemicals, substances that will induce taste aversion, or other compounds designed to reduce levels of rodent damage (Prakash, 1988; Massei *et al.*, 2002; Baldwin *et al.*, 2016; Allsop *et al.*, 2017; Witmer, 2022). However, as food preferences and food aversions may be socially induced in some pest species, such as the Norway rat (*Rattus norvegicus*), baits need to be formulated such that they are not only palatable but slow-acting so that associative avoidance of baits is reduced (Galef & Wigmore, 1983; Heyes & Galef, 1996; Solomon *et al.*, 2002 *cf.* Galef *et al.*, 2006). In these situations, baits comprised of familiar or natural food types are usually eaten in greater quantities than unfamiliar or synthetic baits (e.g., Morriss *et al.*, 2008; Samaniego et al., 2021).

Less research has been carried out on the effects of food familiarity on non-pest rodents, but learnings from management studies are likely to be still applicable. For example, granivorous rodents may have stronger preferences for familiar seeds as they are better suited to fulfil their nutritional requirements (Kelrick *et al.*, 1986). Rodents also are likely to choose familiar seeds because they encounter them frequently under natural circumstances, and recognize and handle these species quickly and efficiently (Kotler & Brown, 1988). Granivores do not always differentiate or select familiar native seeds over unfamiliar exotic seeds (Blaney & Kotanen, 2001), but there are many examples where they do. In North America, Shahid *et al.* (2009) found that rodents mainly selected native plant seeds over seeds from non-native plants, while Rose *et al.* (2014) reported the white-footed mouse (*Peromyscus leucopus*) to have a higher preference for native fruits than those of the invasive Morrow's honeysuckle (*Lonicera morrowii*). Everett *et al.* (1978) also found that, under laboratory conditions, deer mice (*Peromyscus maniculatus*) showed a high preference for seeds from commonly planted rangeland species, with other seeds eaten only if the usually common and thus familiar species were not available.

In Australia, laboratory studies suggest that most native rodents—including desert species—will eat a wide range of seeds, fruits, insects, green plant leaves, root vegetables and commercially prepared rodent foods such as mouse cubes (Watts, 1982a,b; Jackson *et al*., 2023). If presented with arrays of exotic and unfamiliar seeds, species such as the spinifex hopping-mouse and *P. hermannsburgensis* consume some seed species more than others, suggesting that preference for, and familiarity with, certain foods can develop quickly (Murray & Dickman, 1994b). Clear preferences can emerge also in trials using native seeds with which these latter species are familiar, with *P. hermannsburgensis* preferring native seeds with a relatively high water content in one of two captive trials run by Murray and Dickman (1997). In all captive situations, however, rodents have little option but to consume the foods they are presented with, or starve. Laboratory studies thus provide limited insight into the factors that influence seed selection in rodents under natural conditions, especially context-dependent factors such as familiarity with the suites of food resources that are available within the landscapes that the foragers inhabit. In this chapter, field experiments are described that aim to better understand the role that familiarity may play in the selection of native seeds by *P. hermannsburgensis*.

The field experiments were carried out in two different sites where *P. hermannsburgensis* was known to occur from concurrent live-trapping studies (Dickman *et al*., 2014; Greenville *et al*., 2016), but which differed markedly in plant species composition and hence the arrays of seed species that would be available, and familiar, to *P. hermannsburgensis*. Assuming that the seeds are edible and provide some level of energetic return to the rodents, two predictions can be made that follow expectations based on concepts of both food-familiarity and classical foraging theory (Stephens & Krebs, 1986). Thus, *P. hermannsburgensis* should: 1) select seed species in correspondence with their likelihood of encountering them while foraging, and 2) differ in their choice of seed species between disparate sites. Following the findings presented in Chapters 3 and 4, seed species are used that are known to be eaten by *P. hermannsburgensis*, and attempts are made to minimize the influence of extrinsic factors such as predation risk that could potentially affect seed selection.

Methods

Study site

Research was conducted on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E). The landscape has long parallel sand dunes up to 8 m high and 0.5-1 km apart with hard claypans forming between the dunes (Wardle *et al*., 2015). The major vegetation is spinifex *Triodia basedowii* with ephemerals and perennial shrubs dominating the dune crests such as *Crotalaria* spp. and *Grevillea* spp.; in the swales there are stands of trees such as mulga *Acacia aneura* and Georgina gidgee *Acacia georginae* (Wardle *et al*., 2015).

As described in previous chapters, the average annual rainfall can vary greatly between dry and unproductive 'bust' years and wet 'boom' years, with most rainfall occurring in summer (Dickman *et al*., 2010; Greenville *et al*., 2013). The long-term average is 199 mm/year, recorded at Marion Downs (a station located 120 km from Ethabuka). During 2016 and 2017, when the present study was carried out, rainfall was above average in 2016 (370 mm) but average in 2017 (205 mm); rainfall data obtained from a weather station at the study sites (Environdata, Warwick, Qld). Although on-site weather station data were available for only 20 years at the time of study, annual rainfall records from this station and from Marion Downs were highly correlated ($P < 0.001$) and thus can be considered reliable. Temperature varies widely depending on season, with average daily temperature exceeding 40°C in summer and often falling below 5°C during winter (Greenville & Dickman, 2005).

For the experiments reported here, two sites were selected that differed in their plant species composition. The first site, Site 1, was dominated by *T. basedowii* which had flowered and set seed prior to the first trial that was carried out in September 2016. Shrubs such as *G. stenobotrya* occurred commonly, with occasional *Acacia ligulata*, *Dodonaea viscosa* and *Eremophila longifolia*. Large patches of ephemeral herbs and forbs had also flowered and produced seeds following winter rains, notably *Trachymene glaucifolia*. Other ephemerals such as *Calandrinia balonensis, Haloragis gossei, Goodenia cycloptera* and *Oldenlandia pterosporum* also occurred sporadically. The second site, Site 2, was located ~6 km north of the first, a distance considered sufficient to ensure a degree of independence from the first with a low likelihood of any movement of individual animals between them. Although also dominated by *T. basedowii*, no seed production at this site had occurred; flower spikes were present on some hummocks but none was found with evidence of fresh or old seed (Wright *et* *al*., 2014). The dominant shrubs at this site were *Acacia dictyophleba* and *Dicrastylis costelloi*, with occasional *Grevillea juncifolia*, *A. ligulata* and *Eucalyptus pachyphylla*. Winter rains had produced flushes of flowering and seed production by ephemerals such as *Calandrinia balonensis*, *Ptilotus polystachyus* and, in particular, *Trianthema pilosa*. These floristic differences between the sites were considered to be potentially sufficient to have also produced disparate seed banks.

Study species

The sandy inland mouse (*Pseudomys hermannsburgensis*) is a small (12 g), nocturnal, quadrupedal native Australian rodent with a wide distribution covering most of arid Australia. It generally prefers microhabitats that provide dense cover and, in the Simpson Desert, forages mainly on dune sides and in the swales between sand dunes, whereas the larger (30 g) spinifex hopping-mouse *Notomys alexis* forages primarily on or near the dune crests (Predavec, 1994, 1997). The biology of *P. hermannsburgensis* has been described in more detail in previous chapters.

Field sampling and experiments

Seeds in the soil seed bank

To confirm whether the two study sites did indeed contain disparate seed banks, and to identify and quantify the seeds most, and least, likely to be encountered by *P. hermannsburgensis* while foraging, soil samples were collected on four occasions. The first occasion, in June 2016, was a pilot trial intended to identify seeds in the seed bank at the two study sites. Subsequent sampling was carried out on the same three occasions (September 2016, April 2017 and September 2017) that seed choice trials were undertaken. In June 2016, 12 soil samples were taken from the swales and lower dune sides at each site using a rigid, square, metal quadrat (20 × 20 cm). The sides of the quadrat were 2 cm deep, allowing soil to be excavated to this depth, following the findings of Chapter 5 that deeper seeds are exploited infrequently by mice. The position of each sample was determined by throwing the quadrat haphazardly; the main criterion was that sample locations had to be at least 20 m apart to ensure a degree of independence, but the tool was thrown again if it had chanced to land on top of a large spinifex hummock or shrub. Samples were sieved in the field through a prospector's type-A 200 mm diameter sieve with 530 µ mesh to remove fine sand and retain all but the tiniest seeds (such as those of *Portulaca* spp.), and the remaining sample (usually 5–15 ml) placed in a plastic zip-lock bag for transport and later analysis. These samples were spread out on white dishes in the laboratory, and all seeds carefully removed using a fine paintbrush and forceps. Care was taken to discard seeds that had been partially eaten or damaged, with only intact seeds retained for analysis. These seeds were counted and identified by reference to an extensive seed herbarium for Ethabuka, as described by Burns *et al*. (2015). The same procedure was followed in September 2016, April 2017 and September 2017 when seed choice experiments were also being run, except that the sample size at each of the two sites on each occasion was doubled, from 12 to 24.

Seed choice experiments

As in Chapter 4, 'cafeteria' style seed choice experiments were conducted. At each site 12 round seed plates (bucket lids, 30 cm diameter) were set up. To maximize the opportunity for these to be encountered by the target *P. hermannsburgensis*, plates were positioned on the lower slopes of dunes and in the swales where these mice are most active (Predavec, 1994). The plates were spaced ~20 m apart from each other and near the edge of a spinifex hummock to provide a sheltered microhabitat for visiting rodents to forage with reduced risk of predation. The sand in a radius of 10 cm around the plates was swept and smoothed so that the footprints and hence identity of visiting rodents would be captured. As in Chapter 4, the chance of ant visits to the seed plates was reduced by elevating the plates ~5 cm above the sand surface. Rather than using wooden tripods to elevate the seed plates, however, the plates were glued on top of a PVC cylinder (16 cm wide) to provide a strong and stable base. To further deter ants, the cylinder was smeared with a mixture of Vaseline and Coopex insecticide powder (Bayer Ltd, Pymble, Sydney). *P. hermannsburgensis* were readily able to access the elevated plates, as confirmed by direct observations and footprints of the mice on the smoothed sand. The plates were provided with a shallow (0.5 cm) layer of sand to provide a familiar substrate for any mice that accessed them.

Following analysis of the abundance, dispersion and composition of the seeds in the soil seed bank at each site (see below), seven species of seed were identified to provide a test of the study's predictions: spinifex (*Triodia basedowii*), *Grevillea stenobotrya*, *Goodenia cycloptera*, *Trachymene glaucifolia*, *Acacia dictyophleba*, *Dicrastylis costelloi* and

Trianthema pilosa. Half of these species were common and the other half uncommon in one site, whereas the reverse was true at the other site. Thus, at Site 1 *T. basedowii*, *G. stenobotrya* and *T. glaucifolia* were common seeds and *A. dictyophleba*, *D. costelloi* and *T. pilosa* were rare. At Site 2, *A. dictyophleba*, *D. costelloi* and *T. pilosa* were common seeds and *T. basedowii, G. stenobotrya, G. cycloptera* were rare. *Trachymene glaucifolia* was replaced with *G. cycloptera* at Site 2 as *T. glaucifolia* was moderately common at the second site, thus ensuring there was a balance of three common and three rare species at each site. A small, measured amount (~0.5 g) of the six different seed species at each site was placed individually into small (5 cm diameter, 1 cm deep) Petri dishes that were arranged in random positions on each seed plate. The dishes were set up in the late afternoon before nightfall and checked at or just before first light each morning for four consecutive days. All seeds on any plates with evidence of rodent activity based on footprints left on the sand were removed and reweighed to calculate the amounts of seed taken overnight; any seeds that had been removed were replenished.

To account for differences in seed mass not caused by rodent foraging, such as environmental or climatic factors (e.g., wind, humidity, invertebrate predation), a control plate was set up at each site every night the experiments were run. The control plates were set up in an identical manner to the experimental plates, with the same seeds, but were fitted with a wire mesh cage (1-cm square mesh) enclosing the plates to prevent rodent access. Seeds on the control plates were removed and reweighed each morning. Any mass changes detected could then be attributed to environmental factors rather than rodent predation, and used to correct the true seed loss due to rodent predation on seeds on the open experimental plates. Experimental and control seeds were freshly collected in the study area when possible, but older seed collected over the previous 1–2 years was used if sufficient fresh seed could not be found. The same experimental approach was repeated three times on field trips during September 2016, April 2017 and September 2017.

Seed quality

All seed species used in the experiments above have been observed to be eaten by *P. hermannsburgensis* (Chapter 3; Murray & Dickman, 1994a, 1997) and were thus known to be edible. To gauge whether seed quality might interact with seed familiarity to influence seed selection in *P. hermannsburgensis*, seeds were assayed for energy and water content. The water content of seeds was determined by drying batches of seeds at 100°C to constant weight (Murray & Dickman, 1997). The energy content of the seeds was determined using a bomb calorimeter (model PARR 1109A) as per the user instruction manual (https://www.parrinst.com/products/sample-preparation/oxygen-combustion-bombs/semi-micro-oxygen-combustion-bomb-model-1109a/documents/). In brief, 0.221–0.224 g of dry seed was placed in the calorimeter crucible, the fuse added to the crucible lid, and the crucible assembly placed into a moistened bucket prior to ignition of the sample. The resultant temperature change allowed calculation of the energy yield via the formula: energy equivalent × temperature change (-fuse weight left)/ mass. Four replicates for each seed species were assayed for water and energy content.

Statistical analyses

Seed water and seed energy content were compared between the seven selected seed species using 1-factor analysis of variance (ANOVA), after first confirming homogeneity of variances using Levene's test (Quinn & Keough, 2002). To test the first prediction, that *P. hermannsburgensis* should select seed species in correspondence with their likelihood of encountering them while foraging, encounter probability was assumed to be, potentially, a function of i) seed numbers, ii) seed dispersion (clumped or dispersed - dispersed seed should encountered more frequently than clumped seeds) or iii) biomass, or combinations thereof. These quantities are expressed simply as i) the total number and mean ± SD of each seed species recorded in the 24 soil seed samples per site (and 12 samples in the pilot sampling), ii) the coefficient of variation (CV) in seed numbers within the samples from each site, and iii) the overall biomass of each species estimated by multiplying seed number by mean dry biomass measured in the present study and Burns *et al*. (2015). To examine the response of *P. hermannsburgensis* in the seed choice experiments, I used 1-factor ANOVAs to compare the amount (mass) of the three seed species likely to be encountered most frequently by mice in the soil seed bank against three species that were likely to be encountered infrequently. Initial tests pooled seed-take of the three common species for comparison against the three rare species at each site, and further tests compared the amounts of each seed species taken. *Post hoc* Tukey tests were used to identify differences between species in tests where $\alpha \leq 0.05$ (Quinn & Keough, 2002). To test the second prediction, that *P. hermannsburgensis* will differ in their choice of seed species between disparate sites, paired-sample *t*-tests were used. Univariate statistical summaries were carried out using JMP 16.0 (Goos & Meintrup, 2015; SAS, 2020), and inferential tests were carried out using R version 4.2.2 (R Development Core Team, 2018). All results are ± SD unless otherwise stated.

Results

Pilot seed sampling

The pilot seed sampling trial in June 2016 indicated that three species were most abundant at Site 1 and three others at Site 2. At Site 1 *Triodia basedowii* (8.33 ± 4.19 seeds / quadrat), *Grevillea stenobotrya* (6.83 ± 5.98) and *Trachymene glaucifolia* (7.50 ± 8.65) were recorded most frequently, while at Site 2 the most common seeds were *Acacia dictyophleba* (5.67 ± 5.88 seeds / quadrat), *Dicrastylis costelloi* (9.50 ± 3.92) and *Trianthema pilosa* (12.17 ± 10.73). Except for *T. glaucifolia* at Site 2 (0.58 ± 1.38 seeds / quadrat), the three seed species that were most common at each site were among the rarest at the other site and represented there by only 1–2 seeds in 12 samples. Because *T. glaucifolia* was relatively common at Site 2, *Goodenia cycloptera* (1 seed found in the 12 samples at Site 2) was substituted as a further potential rare species to use in the subsequent seed choice experiments. These seven seed species could be collected readily in the field, making them potentially suitable for use in the seed choice experiments. In total, 25 other seed species were found at Sites 1 and 2, varying in total numbers from 1–43 per site (0.08–3.58 / quadrat. Although some of these, such as seeds from the grass *Aristida contorta*, herb *Ptilotus polystachyus* and shrub *Sida fibulifera* could also be collected readily, they were relatively common and widespread at both Sites 1 and 2, and hence not appropriate for the seed choice experiments.

Seed quality

The mean energy content of the seven seed species identified in the pilot trial varied from 17.79–23.30 kJ/g (Table 1), but relatively high variation in values within most species resulted in no statistically significant difference between seeds ($F_{6,21}$ = 1.978, P = 0.115). Water content also was variable between the seed species (Table 1), but again not significant ($F_{6,21}$ = 1.736, P = 0.162).

Table 1. Energy and water contents of seven seed species sampled in the Simpson Desert, central Australia, for use in seed choice experiments. Data are shown as means ± SD, with *n* = 4 for each sample.

Plant seed species	**Energy density (kJ/g)**	**Water (%)**
Triodia basedowii	18.25 ± 0.80	6.48 ± 1.71
Grevillea stenobotrya	23.30 ± 3.75	8.53 ± 1.90
Trachymene glaucifolia	19.79 ± 2.37	9.35 ± 2.37
Goodenia cycloptera	20.83 ± 3.94	6.78 ± 1.57
Acacia dictyophleba	19.60 ± 2.07	10.12 ± 3.46
Dicrastylis costelloi	19.83 ± 1.84	8.63 ± 0.59
Trianthema pilosa	17.85 ± 1.60	8.95 ± 1.22

Seeds in the soil seed bank

Seeds recovered from soil samples taken in September 2016 reflected the same patterns of commonness and rarity at each site as were identified in the pilot sampling (Table 2). At Site 1, *T. basedowii*, *G. stenobotrya* and *T. glaucifolia* were the most frequently recovered seeds, whereas at Site 2 the most common species were *A. dictyophleba*, *D. costelloi* and *T. pilosa* (Table 2). Other seed species (*n* = 22 in addition to the focal seed species) varied in overall abundance from 1–16 at Site 1 and from 1–29 at Site 2. The more even representation of seeds between samples resulted in lower CVs for common than for rare seed species, and overall biomass for the common species was also much higher than for the rare species (Table 2).

Table 2. Seeds recovered from the soil seed bank in September 2016 from two sites in the Simpson Desert, central Australia. Shading indicates species used in concurrent seed choice experiments: grey shading = species considered to be common in that site, blue shading = species considered to be rare, no shading = the species was not used in that site.

	Site 1 - Sept 2016				**Site 2 - Sept 2016**			
Plant seed species	No.*	Mean ± SD	CV	Biomass (mg)**	No.*	Mean ± SD	CV	Biomass (mg)**
Triodia basedowii	115	4.792 ± 5.83	121.6	310.5	3	0.125 ± 0.34	270.3	8.1
Grevillea stenobotrya	86	3.583 ± 3.43	95.6	2003.8	1	0.042 ± 0.20	489.9	23.3
Trachymene glaucifolia	102	4.25 ± 5.51	129.7	295.8	33	1.375 ± 3.03	220.6	95.7
Acacia dictyophleba	2	0.083 ± 0.28	338.8	48.8	90	3.75 ± 5.75	153.4	2196
Dicrastylis costelloi	3	0.125 ± 0.34	270.3	37.5	174	7.25 ± 8.61	118.8	2175
Trianthema pilosa	1	0.042 ± 0.20	489.9	2.6	137	5.708 ± 8.88	155.6	356.2
Goodenia cycloptera	6	0.25 ± 0.53	212.6	7.5	2	0.083 ± 0.28	338.8	2.5

*No. = total number of seeds of each species recovered from 24 samples per site. **Biomass = dry biomass of each seed species pooled over the 24 samples per site.

In April 2017 the distribution of common and rare seed species paralleled that seen in September 2016, although overall seed numbers were more variable (Table 3). The overall biomass of common species was generally greater than that for other seed species, and the generally lower CVs of these species reflected their uniform distribution within each site as compared with the rare seed species. Twenty-seven further seed species were recorded across both sites in addition to the seven focal species, ranging in total numbers from 1–43 at Site 1 and from 2–30 at Site 2.

Table 3. Seeds recovered from the soil seed bank in April 2017 from two sites in the Simpson Desert, central Australia. Shading indicates species used in concurrent seed choice experiments: grey shading = species considered to be common in that site, blue shading = species considered to be rare, no shading = the species was not used in that site.

Plant seed species	**Site 1 - April 2017**				**Site 2 - April 2017**			
	No.*	Mean ± SD	CV	Biomass (mg)**	No.*	Mean ± SD	CV	Biomass (mg)**
Triodia basedowii	130	5.417 ± 7.17	132.4	351.0	0	-	-	-
Grevillea stenobotrya	77	3.208 ± 4.64	144.7	1794.1	4	0.167 ± 0.48	288.9	93.2
Trachymene glaucifolia	158	6.58 ± 10.02	152.2	458.2	19	0.792 ± 1.21	153.5	55.1
Acacia dictyophleba	5	0.208 ± 0.51	244.3	122.0	42	1.75 ± 2.72	155.6	1024.8
Dicrastylis costelloi	1	0.042 ± 0.20	489.9	12.5	239	9.958 ± 14.99	150.5	2987.5
Trianthema pilosa	3	0.125 ± 0.61	489.9	7.8	65	2.708 ± 5.70	210.4	169.0
Goodenia cycloptera	17	0.708 ± 1.73	244.5	21.3	4	0.167 ± 0.48	288.9	5.0

*No. = total number of seeds of each species recovered from 24 samples per site. **Biomass = dry biomass of each seed species pooled over the 24 samples per site.

In September 2017 a similar pattern of common versus rare seed species was documented in each site to those observed in earlier sampling periods (Table 4). Overall seed numbers were lower, although this was in part the result of the loss during transit of seven samples from Site 1 and six samples from Site 2. In addition to being present in greater numbers, common seeds again were characterized by having greater overall biomass and lower CVs than the rare species at each site (Table 4). An additional 21 seed species were identified in total from the two sites, with total seed numbers per species ranging from 1–19 at Site 1 and 1–25 at Site 2.

Table 4. Seeds recovered from the soil seed bank in September 2017 from two sites in the Simpson Desert, central Australia. Shading indicates species used in concurrent seed choice experiments: grey shading = species considered to be common in that site, blue shading = species considered to be rare, no shading = the species was not used in that site.

	Site 1 - September 2017				**Site 2 - September 2017**			
Plant seed species	No.*	Mean ± SD	CV	Biomass (mg)**	No.*	Mean ± SD	CV	Biomass (mg)**
Triodia basedowii	53	3.118 ± 3.81	122.1	143.1	1	0.056 ± 0.24	424.3	2.7
Grevillea stenobotrya	39	2.294 ± 3.44	150.0	908.7	1	0.056 ± 0.24	424.3	23.3
Trachymene glaucifolia	35	2.059 ± 2.79	135.7	101.5	16	0.889 ± 1.23	138.5	46.4
Acacia dictyophleba	2	0.118 ± 0.49	244.3	48.8	57	3.167 ± 3.37	106.3	1390.8
Dicrastylis costelloi	2	0.118 ± 0.33	282.3	25.0	47	2.61 ± 4.86	186.3	587.5
Trianthema pilosa	1	0.059 ± 0.24	412.3	2.6	45	2.500 ± 2.77	110.8	117.0
Goodenia cycloptera	13	0.765 ± 1.39	182.2	16.3	0	-	-	-

*No. = total number of seeds of each species recovered from 17 samples at Site 1 and 18 samples at Site 2. **Biomass = dry biomass of each seed species pooled over all the samples per site.

Seed choice experiments - Site 1

Seed-take in the first trial at this site in September 2016 was relatively low and dominated by the removal of *G. stenobotrya* seeds (Fig. 1). Overall, the three most common seeds in the seed bank at Site 1 were taken from the seed dishes in greater amount (0.548 ± 0.779 g per night) than were the three rare seed species (0.005 ± 0.0173 g) ($F_{1,22}$ = 5.841, *P* = 0.034). Comparison among the individual seed species confirmed the importance of *G. stenobotrya* and then *T. basedowii* as the species that were most consumed (Table 5).

In April 2017 more *G. stenobotrya* and *A. dictyophleba* were removed than any other seed species from Site 1 (Fig. 2). Removal of the three most common seed species in the seed bank at this site (2.293 ± 2.095 g per night) tended to be greater than removal of the rare seeds (1.368 ± 1.829 g), but the difference was not statistically significant ($F_{1,22}$ = 1.327, *P* = 0.262). Comparison among the different individual seed species confirmed that *G. stenobotrya* and *A. dictyophleba* were removed more than any other species (Table 5).

Results in September 2017 at Site 1 were similar to those from April, with *G. stenobotrya* and *A. dictyophleba* being the dominant species removed (Fig. 3). Overall removal of the three most common seeds in the seed bank (2.855 ± 2.101 g per night) tended to be greater than the removal of the three rare seeds (1.793 ± 1.692 g), but was not significantly so ($F_{1,22}$ = 1.858, *P* = 0.187). comparison of removals of the individual seed species showed that *G. stenobotrya* was taken more than any other species, followed by *A. dictyophleba* (Table 5).

Pooling the three common seed species at Site 1 over the three separate experimental trials showed that their average nightly removal by *P. hermannsburgensis* was 1.897 ± 1.989 g compared with 1.056 ± 1.597 g for the rare seed species; this difference bordered on significance ($F_{1,70}$ = 3.918, *P* = 0.051).

Table 5. Total amount of six plant seed species removed from experimental dishes (mean ± SD per night) from one site (Site 1) in the Simpson Desert by the sandy inland mouse (*Pseudomys hermannsburgensis*).

	Common in seed bank			**Rare in seed bank**				
	Triodia basedowii	*Grevillea stenobotrya*	*Trachymene glaucifolia*	*Acacia dictyophleba*	*Dicrastylis costelloi*	*Trianthema pilosa*	*F*	df
Sept 2016	^{a,b}0.105 ± 0.21	^{b}1.523 ± 0.523	0	0	^{a}0.015 ± 0.03	0	26.91***	2,9
April 2017	^{a}0.408 ± 0.201	^{b}4.80 ± 1.366	^{a}1.673 ± 0.749	^{b}3.585 ± 1.546	^{a}0.220 ± 0.136	^{a}0.30 ± 0.170	18.48***	5,18
Sept 2017	^{a}1.04 ± 0.911	^{b,c}5.505 ± 0.693	^{a}2.02 ± 0.445	^{b}3.807 ± 0.952	^{a}0.448 ± 0.416	^{a}1.125 ± 1.00	25.44***	5,18

*** $P < 0.001$. ANOVA for September 2016 omitted data for *Trachymene glaucifolia*, *Acacia dictyophleba* and *Trianthema pilosa* as no seed from these species was taken. Different superscript letters indicate means that differed in *post hoc* Tukey tests.

Seed choice experiments - Site 2

In September 2016 there was relatively little seed-take from this site, but small amounts of each of the species that were found most commonly in the seed bank were consumed (Fig. 1). More seed was taken from the three common seed species together (0.0975 ± 0.107 g per night) than from the rare seed species (0.0183 ± 0.042 g) ($F_{1,22} = 8.027$, $P = 0.009$), although no differences between the six individual seed species were detected (Table 6).

In April 2017 there was moderate removal of all seed species from Site 2 except *T. basedowii* (Fig. 2). However, there was no difference in the collective removal of common vs rare species at this site (common: 1.392 ± 0.796 g per night; rare: 1.247 ± 1.328 g; $F_{1,22} = 0.104$, $P = 0.75$), nor when consumption of the six separate seed species was compared (Table 6).

Results in September 2017 at Site 2 were similar to those from April. Overall removal of the three most common seed species at the site (1.821 ± 1.548 g per night) tended to be greater than removal of the three rare species (1.088 ± 1.253 g), but was not significant ($F_{1,22}$ =

1.624, $P = 0.216$). No differences in consumption were found across the six seed species (Table 6).

Pooling the three common seed species at Site 2 over the three separate experimental trials showed that their average nightly removal by *P. hermannsburgensis* was 1.104 ± 1.227 g compared with 0.785 ± 1.164 g for the rare seed species; a non-significant difference ($F_{1,70} = 1.284$, $P = 0.261$).

Table 6. Total amount of six plant seed species removed from experimental dishes (mean ± SD per night) from one site (Site 2) in the Simpson Desert by the sandy inland mouse (*Pseudomys hermannsburgensis*).

	Rare in seed bank		**Common in seed bank**					
	Triodia basedowii	*Grevillea stenobotrya*	*Goodenia cycloptera*	*Acacia dictyophleba*	*Dicrastylis costelloi*	*Trianthema pilosa*	*F*	df
Sept 2016	0.035 ± 0.07	0.008 ± 0.015	0.013 ± 0.025	0.143 ± 0.132	0.073 ± 0.095	0.085 ± 0.081	1.879	5,18
April 2017	0.253 ± 0.154	2.260 ± 1.649	1.230 ± 1.018	1.83 ± 0.946	1.03 ± 0.711	1.315 ± 0.697	2.013	5,18
Sept 2017	0.522 ± 0.402	2.290 ± 1.497	0.453 ± 0.683	2.325 ± 1.700	1.983 ± 1.814	1.155 ± 1.319	1.661	5,18

No ANOVAS were significant; *P*-values ranged from 0.126 – 0.195.

Seed choice experiments - comparison between sites

Comparisons of the seeds eaten by *P. hermannsburgensis* between the two sites (with *T. glaucifolia* in Site 1 compared against *G. cycloptera* in Site 2) revealed no differences within the three experimental occasions (September 2016: $t_5 = 0.82$, $P = 0.45$; April 2017: $t_5 = 0.89$, $P = 0.41$; September 2017: $t_5 = 1.32$, $P = 0.24$) or when results were pooled across the three occasions ($t_{17} = 1.81$, $P = 0.087$).

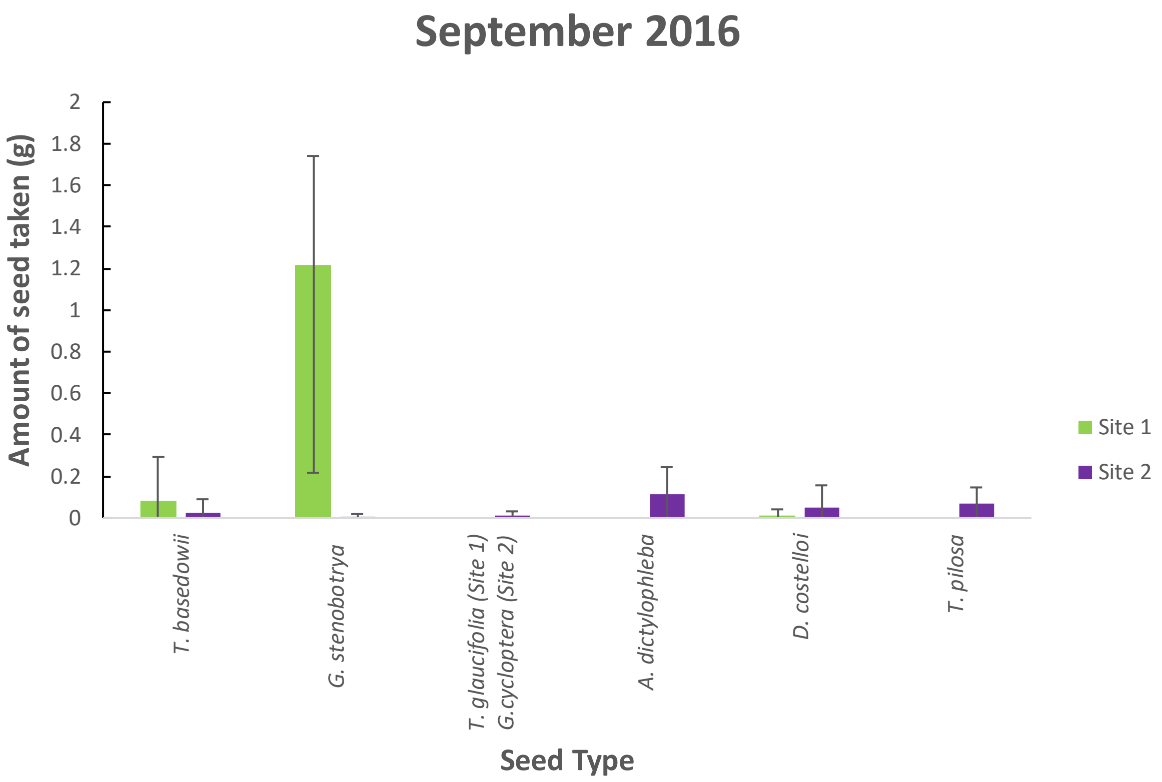

Figure 1. Consumption of seven species of native seeds by sandy inland mice (*Pseudomys hermannsburgensis*) in the Simpson Desert, central Australia, expressed as the mean ± SD amount of seed taken (g) per night per seed species, in September 2016. Three seed species were considered to be common in the local seed bank and three rare at Site 1, with the same species being reversed in their relative abundance at Site 2.

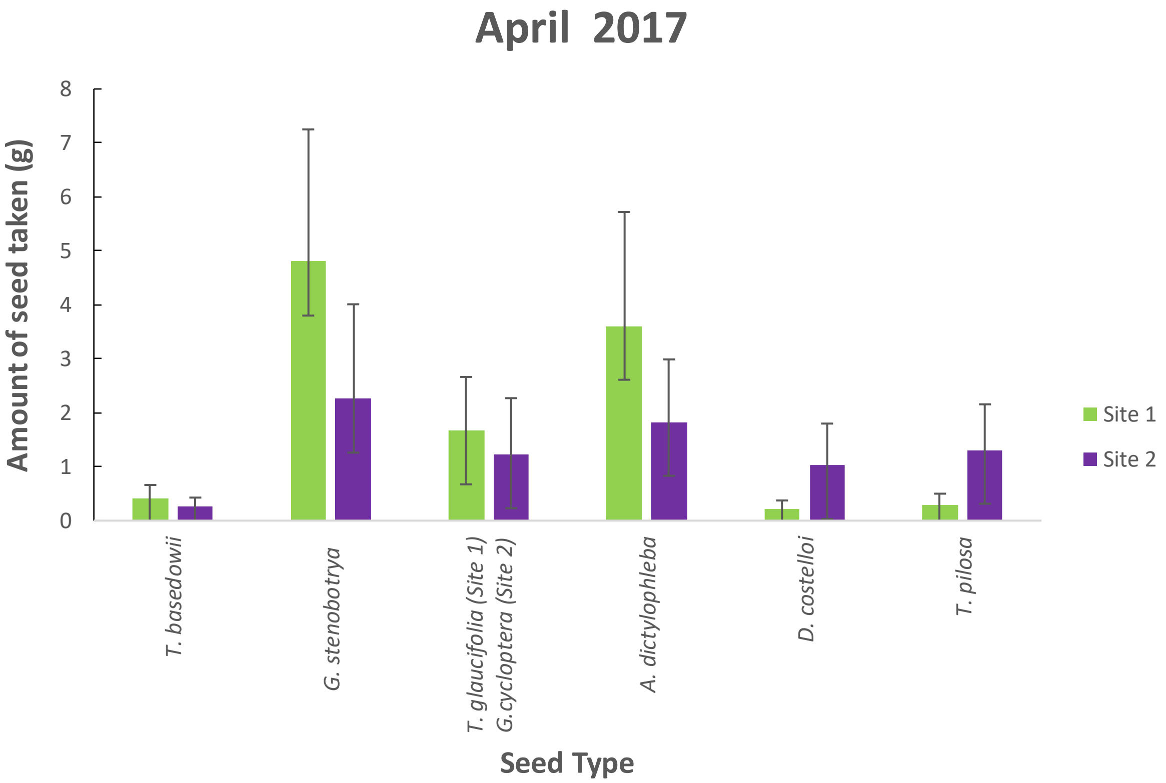

Figure 2. Consumption of seven species of native seeds by sandy inland mice (*Pseudomys hermannsburgensis*) in the Simpson Desert, central Australia, expressed as the mean ± SD amount of seed taken (g) per night per seed species, in April 2017. Three seed species were considered to be common in the local seed bank and three rare at Site 1, with the same species being reversed in their relative abundance at Site 2.

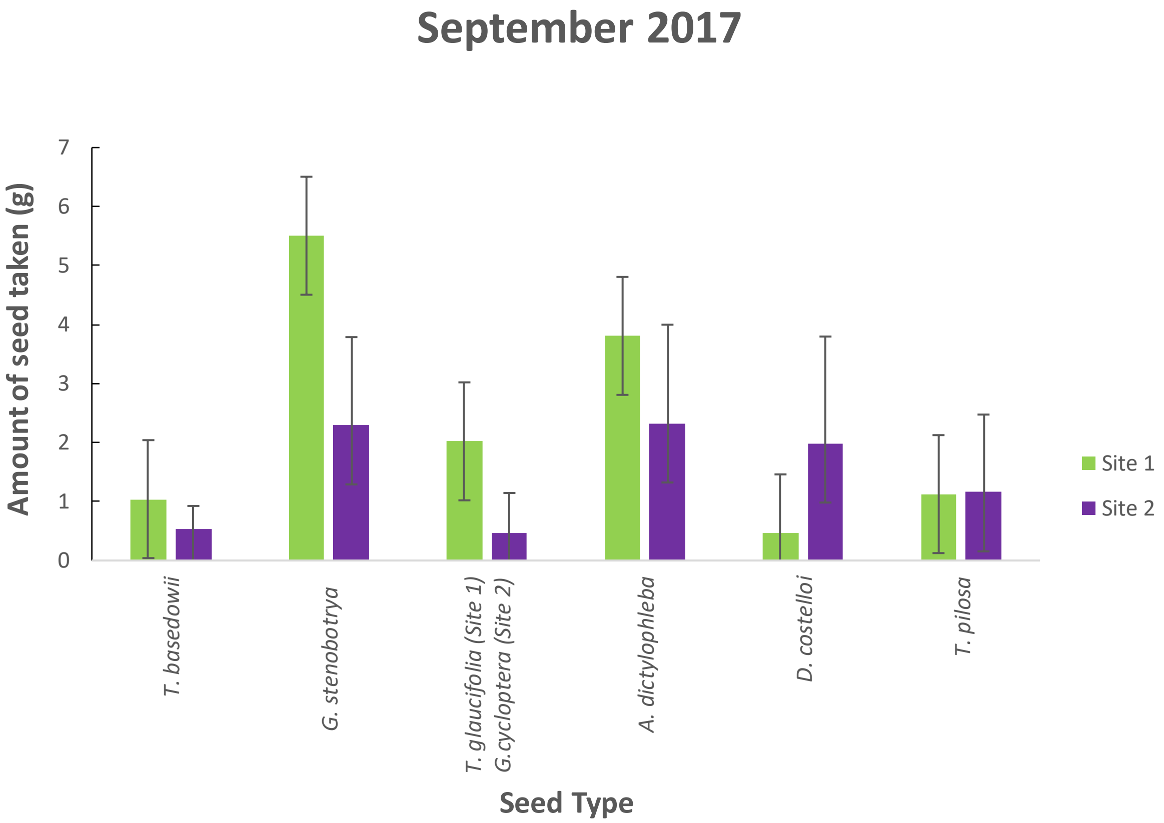

Figure 3. Consumption of seven species of native seeds by sandy inland mice (*Pseudomys hermannsburgensis*) in the Simpson Desert, central Australia, expressed as the mean ± SD amount of seed taken (g) per night per seed species, in September 2017. Three seed species were considered to be common in the local seed bank and three rare at Site 1, with the same species being reversed in their relative abundance at Site 2.

Discussion

The pilot sampling of seeds in the soil seed bank and more extensive sampling during the seed choice experiments confirmed that three seed species were recovered consistently and most abundantly at Site 1, whereas three different seed species were recovered most frequently at Site 2. These species also had higher overall biomasses and were more evenly dispersed (lower CVs) than seed species that were considered to be rare at each site. These differences in seed distribution at each site suggested that the different species should have different likelihoods of being encountered by foraging *P. hermannsburgensis*, providing suitable (and necessary) conditions for the seed choice experiments and test of the first hypothesis. Differences in the distributions of seed species between the two sites provided the conditions to test the second hypothesis. Overall, there was some support for the prediction that mice would select familiar seed species that they would encounter frequently while foraging and ignore less familiar seeds that were rare in the seed bank, but no support for the prediction that mice would select different seeds at sites with disparate seed banks. The seeds used in the choice experiments appeared to be similar in quality, at least in terms of their energy and water content, but as discussed further below, other unmeasured seed characteristics may have contributed to the results.

The seed-take results from September 2016 provided the strongest support for the first hypothesis, with more common seeds than rare seeds being eaten by *P. hermannsburgensis* at each site. Overall rodent numbers in this month appeared to be relatively low in concurrent trapping, with animals showing signs of elevated reproductive activity in the wake of earlier rains (C. Dickman, *pers. comm.*) and overall seed-take being relatively low compared with that seen in 2017 (compare Fig. 1 with Figs 2 and 3). Under these conditions, and with predator activity remaining at low levels from the previous year (Chapter 4), mice may have faced few constraints from competitors and predators in selecting seeds at the dishes and clearly selected more of those seeds with which they were familiar. Familiar foods should be recognised more quickly than unfamiliar foods, and animals will have learned from previous experience that they are safe (e.g., contain no toxins) and profitable to eat (Galef & Giraldeau, 2001). Predator-prey theory also predicts that foragers should focus principally on common food types (i.e., positive frequency dependence: Horst & Venable, 2018), and switch to alternative food types only when preferred food types become scarce, thus exhibiting a type-III response (*sensu* Holling, 1959a,b; Chapter 1; see also Murdoch, 1969; van Baalen *et al*., 2001).

Despite the relatively clear seed-take pattern in September 2016, there was little support for the first hypothesis in the results from April and September 2017. There were trends for common seed species to be taken more frequently than rare species, but none was significant. At Site 1 there was an overall tendency for common seed species to be taken more often than rare species over the three sampling occasions ($P = 0.051$), but no overall pattern was obvious at Site 2. In 2017 rodent numbers and predator activity had increased from the levels seen in 2016 (C. Dickman, *pers. comm.*), perhaps contributing to the general increase in seed consumption (compare Figs 1–3) and the shift in seed preference, as discussed further below. However, several other factors can influence the selection of seeds by rodents such as size, water content, seed coat hardness, ease of consumption and nutritional content/chemical composition (Larios *et al*., 2017), and it is likely that some of these factors came into play during the two trials in 2017.

In the first instance, particular seed species were found to be preferred by *P. hermannsburgensis*, most notably *Grevillea stenobotrya* and *Acacia dictyophleba* regardless of their status as common or rare/foreign, which does not follow the original hypothesis that sandy inland mice will prefer seeds they are familiar with (seeds that are found commonly in seed bank in the area) rather than consume seeds that are rare or foreign. These species were heavily consumed in both sites in 2017 regardless of their relative abundance. Although there were no statistically significant differences in energy or water content among all the seed species used in the experiments, *G. stenobotrya* nonetheless had the highest average energy content whereas *A. dictyophleba* had the highest water content (Table 1). Preliminary power analyses indicated that only three more replicates would have produced statistically significant differences among the seven seed species for seed energy content, with *G. stenobotrya* being the most energetically profitable species; five additional replicate samples would have produced a difference in seed water content, with *A. dictyophleba* standing out as being the 'juiciest' seed. These two seed species were also the largest used in the experiments (~23–24 mg) and would be easy for rodents to consume because they lack an external husk; hence, the net rate of energy or water consumption could be maximised by animals consuming these species. Targeting these seed species irrespective of their relative commonness in the seed banks at the two sites was perhaps more advantageous to foragers in 2017 than 2016 as 2017 was a drier year than 2016 and food may have been more limited in 2017 owing to the elevated numbers of rodents at that time. These between-year differences may also account for the relatively low consumption of *T. basedowii* seeds, especially in 2017. Although this species was found to be highly selected by *P. hermannsburgensis* in cafeteria trials by Murray and Dickman (1997), it had the lowest water content of all the experimental seeds that were used here, as well as only a moderate energy content (Table 1).

A further possible factor accounting for the 2017 results is that the seeds of *G. stenobotrya* and *A. dictyophleba* simply look similar: both are oval-shaped, flattened and brown with no husk. It is plausible that *P. hermannsburgensis* that were familiar with *G. stenobotrya* in Site 1 consumed many seeds of *A. dictyophleba* because they appeared to be superficially familiar, whereas heavy consumption of *G. stenobotrya* seeds in Site 2 occurred because of their similarity to the more familiar *A. dictyophleba*.

Kotler and Brown (1988) and Brown and Kotler (2004) suggested that desert rodents follow key predictions of optimal foraging theory, notably that animals will forage in ways that minimise their risk of predation while simultaneously minimising their risk of starvation and maximising net energy intake. Rodents can reduce the time they spend foraging by selectively choosing higher-energy seeds or seeds that require less time to process and consume (Reichman, 1977). Indeed, seed size and ease of consumption are often important factors dictating selection by rodents, with previous studies finding that several desert species select relatively large seeds (Mittlebach & Gross, 1984; Brown & Heske, 1990; Reader, 1993; Maron *et al*., 2012; Larios *et al*., 2017). However, food-familiarity is also important in shaping diet choice in many species (Hughes, 1993; Shahid *et al*., 2009; Rose *et al*., 2014; Costa *et al*., 2016). Fischer and Türke (2016) found both food-familiarity and nutrient quantity in food to be important determinants of foraging in the bank vole *Myodes glareolus*, with voles preferring seeds that were nutrient-rich but also selecting seeds from common plant species rather than seeds from endangered plants. It is possible that these two imperatives—seed familiarity and consumption of the most profitable foods—both contribute to diet selection in *P. hermannsburgensis* but differ in importance depending on environmental conditions. Seed familiarity thus may be more advantageous when the relative availability of food is high, whereas selection of profitable foods may occur when resources are more scarce. Any such conclusion must be tentative here, however, as only two contrasting years were available for comparison.

The second prediction, that *P. hermannsburgensis* would choose different seed species between sites with disparate seed banks, received no support. Although the seed banks differed markedly between Site 1 and Site 2, all experimental seed species were consumed at both sites, with *A. dictyophleba* and *G. stenobotrya* being most strongly selected. On the one hand, these results may reflect 'partial sampling' whereby mice eat small amounts of several food types that they encounter to learn about their potential value (Murray & Dickman, 1997). Partial sampling, in combination with olfaction, may help animals to distinguish seeds that differ subtly in nutrient, energy or water content (Frank, 1988; Larios *et al*., 2017), allowing them to choose those seeds that best meet their dietary requirements at particular times or in particular places. Indeed, Shahid *et al*. (2009) found that, while their study rodents ate more familiar native seeds than non-native seeds, other factors such as the chemical composition of seeds likely contributed to seed choice.

On the other hand, the consumption of all experimental seeds by *P. hermannsburgensis* may have arisen if all the species were more familiar to foraging animals than had been anticipated, so that all were eaten to greater or lesser extent. Although sampling of the seed bank at the two study sites was reasonably extensive and showed marked differences in seed species abundance and composition, my sampling would still have been limited compared with the area over which individual animals are likely to have foraged. For example, individual *P. hermannsburgensis* have been recorded to move over 400 m within an hour while foraging, and up to several kilometres within days (Dickman *et al*., 1995, 2010). The 6-km distance between Site 1 and Site 2 may have been sufficient to preclude animals moving between them during the course of each experiment but, depending on their extent of movement, the familiarity of individual mice with all seeds during each experiment could have varied more markedly than expected. In this situation, partial consumption of all experimental seeds would not be surprising.

To conclude, the results of this chapter suggest that familiarity can influence the seed species eaten by *P. hermannsburgensis,* but also that this effect can be overridden by other factors—potentially, seed quality (energy, nutrient, water content), palatability or ease of handling—such that familiar seeds may be eaten in preference to rare seeds only under certain conditions. Here, the morphologically similar seeds of *Acacia dictyophleba* (high water content) and *Grevillea stenobotrya* (high energy content) were taken in greater amounts than other seeds irrespective of whether they were rare or common in the seed bank, but only in the second year of the study when environmental conditions are likely to have deteriorated. In the first year of the study, when rainfall was above average and *per capita* food resources were likely to have been relatively high, mice preferentially ate familiar seeds. Although speculative, it may be reasonable to suggest that *P. hermannsburgensis* minimise the time spent foraging, and thus maximise efficiency, by taking familiar seeds when conditions are benign, but select seeds based on attributes such as seed quality when constrained by less favourable environmental conditions and thus minimise the risk of starvation. Experimental testing of this possibility could proceed by taking a commonly occurring and palatable seed species and manipulating its quality (e.g., by varying its water content, adding nutrients) such that control, enhanced and depleted seeds are presented to foragers during times when *per capita* food supply in the landscape is high and low.

Despite the patchy support for my initial hypotheses, the results indicate that *P. hermannsburgensis* responds to ostensibly different factors with respect to particular food types and to shifting conditions in the broader environment. The selectivity shown for particular seed species at particular times also suggests that foraging mice may have effects on the seed bank. Thus, while processes such as wildfire, temperature and rainfall fluctuations and climate change will likely impact the diversity of plants that are available for foraging rodents (e.g., Letnic & Dickman, 2005), consumption of certain seeds by rodents may in turn affect plant population dynamics and community composition (Hulme, 1998; Sih & Christensen, 2001). The effects of rodent foraging on the soil seed bank of the Simpson Desert are considered in the next chapter.

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Chapter 7. Impacts of rodents on the soil seed bank

Abstract

Seed banks play a crucial role in plant population dynamics, shaping plant diversity, community composition and structure in concert with climatic, edaphic and other environmental factors. The seed bank also provides a resource for granivorous animals, and the impacts of these consumers can constitute an additional influence on the seed bank and on subsequent vegetation dynamics. In this study, exclosures were used to determine the effect of granivory by rodents in the Simpson Desert, south-western Queensland, Australia. The two numerically dominant species of the region—the sandy inland mouse (*Pseudomys hermannsburgensis*) and spinifex hopping-mouse (*Notomys alexis*)—include seeds as part of their overall diet, and both species are selective in the seeds that they consume. I predicted that seed species composition would differ between sites where rodents had been excluded compared to sites where they had access, and used fenced exclusion plots, open control and procedural control plots to test this prediction. The abundance and composition of seeds in the seed bank differed between times and treatments for the first seven years (1994–1999) that the experiment was run, with treatment differences occurring between the open control and two other treatments. Following drought-breaking rains in 2000 and 2010–2011, which triggered major flowering and seeding events and eruptions of rodents, seeds collected in 2004 and 2011 differed only between treatments, with the rodent exclosures having both greater numbers of seeds and more species than the open and procedural controls. These results support the prediction that rodents affect the soil seed bank, but suggest that their effects are manifest only after rainfall-induced pulse events when populations increase dramatically. During bust periods, temporal differences in the soil seed bank may be driven by local rainfall or other factors, but not by rodent predation.

Introduction

Seed banks are below-ground repositories of the seeds of vascular plants, and are critical for the regeneration and persistence of plant communities. Although the seeds of some plants are held above ground for prolonged periods, such as those of serotinous trees and shrubs, the seeds of most species are shed or dispersed from parent plants after maturation and fall onto the soil surface. They may remain there, or be further dispersed via zoochory or other processes, or become buried within leaf litter or topsoil following mechanical action by wind or the digging activities of animals. Depending on the species, seeds can remain in the seed bank for a few hours up to many years, germinating when seed dormancy is broken (Fenner, 1985; Leck *et al*., 1989; Baskin and Baskin, 2014). In many desert systems the seed bank is dominated by seeds from annual plant species that germinate and flourish rapidly after rainfall, but smaller numbers of seeds from perennial shrubs and succulents are usually also present (Brown and Lieberman, 1973; Brown *et al*., 1979; Marone and Horno, 1997; Haight *et al*., 2019). The interaction between the stored seed bank, rainfall and the pulse of productivity that follows rain, was first explicitly characterized by Noy-Meir (1973) as the 'pulse-and-reserve' model, and this concept has received much support since (e.g., Whitford, 2002; Reynolds *et al*., 2004; Ward, 2016).

In its original form, the pulse-reserve model was dismissive of interspecific interactions such as competition and predation, with Noy-Meir (1973) arguing that the dynamics of arid-dwelling plant populations and communities largely arose from the independent autecological responses of species to the weather. However, there has since been recognition that plant population dynamics are influenced by many abiotic and biotic factors, with one potentially critical factor being predation on above-ground plant tissues and, especially, the seed bank (e.g., Maron and Simms, 1997; Wada *et al*., 1995; Horst and Venable, 2018). Predation on seeds in the seed bank can affect subsequent plant population growth, age structure, persistence, and the overall dynamics of plant communities (Kauffman and Maron, 2006; Gordon and Letnic, 2016). Ants, birds and rodents have been identified as the major seed predator groups in deserts of the Middle East, North America, South America and South Africa (Munger and Brown, 1981; Abramsky, 1983; Morton, 1985; Kerley, 1991; Pérez *et al*., 2006), with granivorous rodents often having particularly large impacts (Brown and Lieberman, 1973; Brown *et al*., 1979; Maron and Simms, 1997). Fluctuations in rodent populations may cause associated temporal changes in the seed bank (Kjellsson, 1985; Price and Joyner, 1997; Hulme, 1998), while changes in the seed bank conversely can be expected to influence *per capita* food availability to rodents (Dickman *et al*., 1999).

The effects of rodents on seed bank dynamics in Australia's extensive arid landscapes are poorly known, but disparate studies suggest that impacts are likely to be subtle or may manifest over prolonged periods. On the one hand, rodent predation would have little effect on plant dynamics if plants accommodate for seed loss by producing larger quantities of seeds, or if seed density has no impact on seedling recruitment and recruitment is set instead by other factors such as the number of suitable sites or available resources for seed germination (Baskin and Baskin, 2014). If seeds settle in sites that are unsuitable for germination their consumption would similarly have little impact on future seedling recruitment (Maron and Simms, 1997; Bricker *et al.*, 2010), a result similar to the 'doomed surplus' effect in studies of predators and their vertebrate prey (Errington, 1946). Rodents may also have little effect on the seed bank if they predominantly harvest newly-produced seeds (i.e., 'seed rain') before they enter the seed bank (Price and Joyner, 1997). In the Australian context, most desert rodents are considered to be facultative omnivores that take seeds as part of a broader overall diet and, during long dry periods, most species occur at densities that could be expected to place little predatory pressure on seed banks (Morton, 1985; Murray and Dickman, 1994a; Predavec, 1994; Murray *et al.*, 1999). Seed dish experiments comparing seed-take by different granivore groups in arid Australia have commonly found that ants remove more seeds than birds and that birds in turn remove more seeds than rodents (Morton, 1982, 1985; Predavec, 1997), with ants remaining numerous and diverse irrespective of environmental conditions (Gibb *et al.*, 2019, 2022).

On the other hand, some countervailing evidence suggests that Australian desert rodents may indeed have some influence on seed banks. Some 23 species of native rodents occur, or occurred, in arid Australia, with 12 of 16 species that have been subjected to dietary analysis taking seeds as part of the diet; the species with seeds in their diets are *Leggadina forresti*, *Leporillus apicalis*, *Notomys cervinus*, *Notomys fuscus*, *Notomys mitchelli*, *Pseudomys albocinereus*, *Pseudomys apodemoides*, *Pseudomys australis*, *Pseudomys desertor*, *Pseudomys hermannsburgensis*, *Pseudomys occidentalis*, and *Rattus villosissimus* (Murray *et al.*, 1999). Although frequently present at low density, many species are eruptive and can achieve densities exceeding 50 animals per hectare for periods of several months (Plomley, 1972; Southgate and Masters, 1996; Dickman *et al.*, 1999; Greenville *et al.*, 2016; Bennison *et al.*, 2018), providing conditions that likely place seed banks under at least temporary predation pressure. Seed dish experiments show further that when desert rodents occur at moderate densities they remove many more seeds than do ants or birds (Tischler, 1998; Hanke, 2011), while the digging activities of larger species such as the long-haired rat (*Rattus villosissimus*) can have positive and negative local effects on the soil seed bank (Dickman, 2003). Gordon and Letnic (2016) challenged the perception that rodents are unimportant granivores in Australian deserts by showing that a rare desert rodent, the dusky hopping-mouse (*Notomys fuscus*), consumed far more seeds than ants when it was common than when it was rare. These authors also proposed that, over decadal or multi-decadal time scales, rodents could influence both the seed bank and the structure of plant communities (Gordon and Letnic, 2016). Taken together, the above observations suggest that rodents may influence soil seed banks in arid areas in Australia, but also that experiments aimed at quantifying such influence would need to be run over long time periods.

Previous research in the Simpson Desert, central Australia, has shown that two species of native rodent, the sandy inland mouse (*Pseudomys hermannsburgensis*) and the spinifex hopping-mouse (*Notomys alexis*), are numerically dominant over long periods, persisting in low numbers during prolonged dry periods ('busts') but achieving high numbers ('booms') after heavy rainfall events (Dickman *et al*., 1999, 2010, 2011; Greenville *et al*., 2016). A third native species, the long-haired rat, erupts from spatially restricted refuge sites occasionally post-rain, but is otherwise absent from the desert landscape for periods of many years (Predavec and Dickman, 1994; Greenville *et al*., 2012, 2013). All species, notably *P. hermannsburgensis* and *N. alexis,* are omnivorous but include substantial amounts of seed in their diets (Murray and Dickman, 1994a,b; Murray *et al*., 1999). The former species has been confirmed to consume seeds selectively and to take most seeds from the soil seed bank (Chapters 3-6), and it is likely that *N. alexis* forages in a similarly selective manner (McNaught, 1994; Murray *et al*., 1997). Based on these observations, this study explores the effects of rodent foraging on the seed bank at sites in the Simpson Desert, and predicts that seed species composition will differ between sites where rodents have been removed compared to sites where rodents have access. In view of the long time frame likely to be needed to detect any effects, and to incorporate fluctuations in rodent numbers between boom and bust periods, the results reported here are derived from data collected over 17 years.

Methods

Study site

Research was conducted on Ethabuka Reserve (formerly Ethabuka station) in the north-eastern Simpson Desert, western Queensland, Australia (23°46′S, 138°28′E). The landscape has long parallel sand dunes up to 8 m high and 0.5-1 km apart with hard claypans forming between the dunes. The dominant vegetation is spinifex (*Triodia basedowii*) with varied perennial shrubs occurring amid the spinifex cover in the interdune valleys and dominating the dune crests, and ephemeral grasses and herbs appearing after summer or winter rains. Detailed descriptions of the vegetation have been provided in Chapter 2 and by Wardle *et al*. (2015).

The annual rainfall varies greatly between boom and bust years, but averaged 199 mm/year over a 94-year period at Marion Downs, 120 km from Ethabuka. During the period of study, between 1994 and 2011, one boom event occurred in 2000 when almost 500 mm of rain fell, and another occurred in 2010–2011 when 522 mm of rain fell between September 2010 and March 2011. Rainfall in other years during the study averaged 146 mm, with just 71 mm falling in 2002 and 260 mm recorded in both 1998 and 2007 (data obtained from onsite Environdata weather station, Warwick, Queensland; see Greenville and Dickman 2005; Dickman *et al*., 2010). Maximum daily temperatures in summer are 46–49 °C, with winter minima falling to -6°C (Purdie, 1984).

Granivores

The sandy inland mouse and spinifex hopping-mouse are the dominant rodents at the study site, but small numbers of long-haired rats and occasional desert mice (*Pseudomys desertor*), Forrest's mice (*Leggadina forresti*) and house mice (*Mus musculus*) have been recorded (Dickman *et al*., 2014). However, no long-haired rats or Forrest's mice were recorded during the present study, and only very small numbers of desert mice and house mice (< 1% those of *P. hermannsburgensis* and *N. alexis*). Granivorous birds include brown quail (*Coturnix ypsilophora*), flock bronzewing (*Phaps histrionica*), crested pigeon (*Ocyphaps lophotes*), diamond dove (*Geopelia cuneata*), little button-quail (*Turnix velox*), galah (*Eolophus roseicapillus*), little corella (*Cacatua sanguinea*), cockatiel (*Nymphicus hollandicus*), Australian ringneck (*Barnardius zonarius*), budgerigar (*Melopsittacus undulatus*), zebra finch (*Taeniopygia guttata*), painted finch (*Emblema pictum*) and pictorella mannikin (*Heteromunia pectoralis*), with most of these species recorded sporadically when suitable conditions have prevailed (Tischler *et al*., 2013). The most common and reliably present species of granivorous birds are zebra finches (*Poephila guttata*), budgerigars (*Melopsittacus undulatus*) and crested pigeons (*Ocyphaps lophotes*) (Predavec, 1997). Among invertebrates, ants are the major seed predators. Predavec (1997) recorded at least 16 species of granivorous of ants in preliminary sampling, with 10 of these being common (Predavec, 1997); at least double these numbers of granivores were recorded in longer-term sampling by Gibb *et al*. (2018, 2019).

Experiment

To determine the influence of granivorous rodents on the soil seed bank in the study site, experimental plots were set up to either exclude rodents from the soil seed bank or to allow them free access. Similar approaches using exclusion fences have been used previously to quantify the effects of rodents on desert seed banks (e.g., Guo *et al*., 1995; Chen and Valone, 2017). The plots were set up initially by Gayle McNaught as part of a broader Honours program in April 1994 (McNaught, 1994) and then maintained by the authors until 2011 when the experiment was terminated. Three treatments were established: fenced exclosure plots (*n* = 6), open control plots (*n* = 6) and procedural control, or 'fake-fence' plots (*n* = 6). The exclosures measured 3 × 3 m and were constructed using 180 cm star pickets as corner posts that supported a wire mesh fence. Pilot trials had indicated that *N. alexis* could make vertical jumps up to 1 m (McNaught, 1994), so the height of the mesh fence was set at 145 cm above ground. The mesh was buried 15 cm in the soil, with a 10 cm skirt, to prevent animals from burrowing under the mesh to gain access to the exclosures. The mesh size was 0.5 cm × 0.5 cm, small enough to exclude all rodents but large enough to allow free access to most invertebrates. The procedural control, or 'fake', fences were constructed in the same way as the exclosure fences but the bottom of the wire mesh was not dug into the ground, thus allowing rodents to move freely underneath. Open control plots were marked by four posts to demarcate the 3 × 3 m plot area, but had no surrounding mesh. All plots were established in mid-dune sites at least 250 m apart, with plots allocated randomly to treatment. To ensure that the exclosures were not accessed by rodents and that the open and procedural control plots were accessible, strips of double-sided sticky tape were wound around the bases of small shrubs in each plot prior to, and after, soil sampling on field trips and checked for the presence of hairs. Any hairs that were found were removed and the identity of the hair donor confirmed by morphological analysis of the hair cuticle and cross-sectional structure (Brunner and Coman, 1974). Plots were also inspected for any small mammal footprints.

Soil samples were taken from within each plot using a rigid, square, quadrat (20 × 20 cm). Samples taken in 1994 used a stiff plastic quadrat and sampled to a depth of 3 cm. After

1994, a metal quadrat was used and the soil was sampled to a depth of 2 cm. Three samples were taken in haphazardly chosen locations in each plot, and the positions marked on a fine-scale grid map so that these sites were not resampled on subsequent occasions. The samples were sieved in the field through a prospector's type-A 200 mm diameter sieve with 530 µ mesh to remove fine sand and retain all but very small seeds (e.g., *Portulaca* spp.) that were unlikely to form part of the diet of rodents. The residual sample (usually 5–15 ml) placed in a plastic zip-lock bag for transport and later analysis. These samples were spread out on white dishes in the laboratory, and all seeds carefully removed using a fine paintbrush and forceps. Seeds were discarded if they had been partially eaten or damaged, with only intact seeds retained for analysis. These seeds were counted and identified by reference to an extensive seed herbarium for Ethabuka (Burns *et al*., 2015). Seed samples and preliminary identifications of seeds from 1994 were kindly made available by G. McNaught, with subsequent samples and processing carried out by the authors.

Samples from the plots were collected on seven occasions before the large rainfall event in 1999–2000 and on two occasions thereafter. The collection dates were March 1994 (a month prior to the erection of the exclosures), August 1994, May 1996, October 1996, April 1997, September 1997, September 1999, August 2004 and October 2011.

Statistical analysis

To test the prediction that rodents would influence the composition of the soil seed bank, I used a *per*MANOVA (permutational multivariate analysis of variance) on the Bray-Curtis dissimilarity matrix of seed numbers in the samples to compare the three treatments (exclosure, fake exclosure [fake] and open control [control]) over time. To simplify analyses, the three samples per plot were pooled; results initially were examined over the 17-year duration of the sampling, and then separated in subsequent analyses into the period before (1994–1999) and after (2004 and 2011) the large rainfall events in 2000 and 2010–2011. The rainfall in 2000 drove a large increase in primary productivity and in populations of rodents (Letnic *et al*., 2005), as did the rainfall in 2010–2011 (Greenville *et al*., 2016). The *P*-value threshold of significance was set at 0.05 for each test, with 999 permutations; pairwise ADONIS analyses was performed to determine differences between treatments for any *per*MANOVAs that were significant. Differences between treatments were visualized using non-metric multidimensional scaling (nMDS) ordinations, following fourth root transformation of the dissimilarity matrix, with SIMPER used to identify the species that contributed most to between-treatment difference. All analyses were implemented using the vegan package in R version 4.2.2 (R Development Core Team 2018; Oksanen *et al*., 2018).

Results

There was no evidence that the exclosures were breached by rodents at any time. Hairs were retrieved from sticky tape in one exclosure between sampling occasions in April and September 1997, but these were identified as belonging to an insectivorous dunnart (*Sminthopsis* sp., probably *S. youngsoni*). There was no sign of a dunnart in the exclosure when soil samples were collected, and no further evidence of visitation was noted at any time. By contrast, both the fake-fence and open control treatments were visited regularly and consistently by rodents (both *P. hermannsburgensis* and *N. alexis*) throughout the study.

All data: 1994–2011

The soil samples collected over the course of the study yielded 12,527 seeds, 5419 from the exclosure plots, 3262 from the fake-fence plots and 3846 from the open control plots.

Over the nine sampling occasions, *per*MANOVA revealed both date ($df = 8$, $P = 0.001$), and treatment ($df = 2$, $P = 0.001$) to have significant effects on the seed bank, with no date × treatment interaction ($df = 16$, $P = 0.993$).

Pairwise ADONIS results showed the exclosure treatment to differ from the fake fence ($df = 1$, $P = 0.034$) and control treatments ($df = 1$, $P = 0.001$), with the fake and open control treatments also differing ($df = 1$, $P = 0.001$). The pairwise tests showed further that all samples differed from each other based on date, with $P < 0.05$ for all comparisons except between March 1994 and August 1994 ($df = 1$, $P = 0.738$) and August 2004 and October 2011 ($df = 1$, $P = 0.214$).

SIMPER analyses identified 19 seed species that differed between the exclosure and fake treatments, these being *Yakirra australiensis*, *Newcastelia spodiotricha*, *Cleome viscosa*, *Abutilon otocarpum*, *Acacia dictyophleba*, *Eremophila longifolia*, *Enchylaena tomentosa*, *Euphorbia tannensis*, *Acacia murrayana*, *Senna pleurocarpa*, *Lechenaultia divaricata*, *Eucalyptus pachyphylla*, *Eremophila macdonnellii*, *Eucalyptus gammophylla*, *Grevillea juncifolia*, *Atalaya hemiglauca*, *Petalostylis cassioides*, *Stylobasium spathulatum* and *Grevillea striata*. All these species occurred more frequently in the exclosure than in the fake fence treatment.

SIMPER identified six seed species that differed between the exclosure and open control treatments, these being *Crotalaria eremaea*, *Abutilon otocarpum*, *Crotalaria cunninghami*, *Acacia murrayana*, *Tephrosia rosea* and *Eremophila macdonnellii*, with all species again achieving higher abundance than in the control treatment.

SIMPER found eight species to differ different between the fake and control treatments. *Sida fibulifera*, *Euphorbia drummondii*, *Calotis erinacea*, *Eriachne aristidea*, *Haloragis gossei*, *Ptilotus latifolius*, Unknown species A and *Tephrosia sphaerospera* were found in greater numbers in the control than the fake fence treatment.

Following the overall between-time and between-treatment differences, above, further analyses focused on comparing treatments in the two periods before and after the heavy rainfall in 2000.

1994-1999

Overall, 8978 seeds were collected and identified from the seven sampling occasions during this period, 3011 from the exclosure plots, 2667 from the fake-fenced plots and 3300 from the open control plots. Forty-three species were identified.

A *per*MANOVA showed that date ($df = 6$, $P = 0.001$) and treatment ($df = 2$, $P = 0.003$) had significant effects on the seed bank. There was no date × treatment interaction ($df = 12$, $P = 0.994$).

Pairwise ADONIS comparisons between times showed that all samples differed from each other ($P < 0.05$) except between March 1994 and August 1994 ($df = 1$, $P = 0.753$) and between April 1997 and September 1997 ($df = 1$, $P = 0.055$). Comparisons between treatments revealed no difference between the exclosure and fake-fence treatments ($df = 1$, $P = 0.339$), but those between the exclosure and open control ($df = 1$, $P = 0.009$) and fake-fence versus open control treatments ($df = 1$, $P = 0.001$) differed significantly. Ordination using nMDS provided little further clarity, showing considerable clustering of data points with some outliers representing all three treatments (Fig. 1). The relatively high stress value (0.19) suggests that the 2-dimensional configuration represents only a moderate fit between the data and the ordination distances.

Separate ordinations of results from the seven sampling occasions between 1994 and 1999 also showed considerable overlap in data points for the three treatments (Figs 2–8).

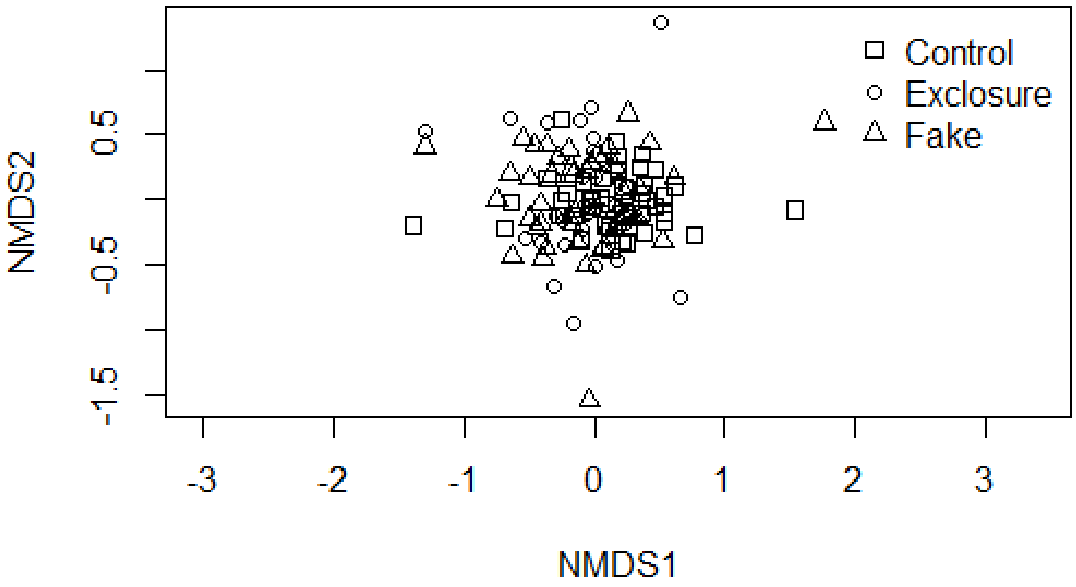

Fig. 1. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert on seven occasions combined between 1994 and 1997 (stress = 0.19).

SIMPER revealed that there were more seeds of *Calotis erinacea* and *Crotalaria eremaea* in the open control versus the exclosure treatments, and differences in six seed species between the fake-fence and open control treatments. The fake-fence treatment contained more seeds of *Scaevola depauperata* and the only seeds of *Scaevola parvifolia*, whereas in the open control treatment *Euphorbia drummondii*, *Crotalaria eremaea*, *Grevillea stenobotrya* and *Ptilotus latifolius* occurred more frequently and in greater amounts than in the fake-fence samples.

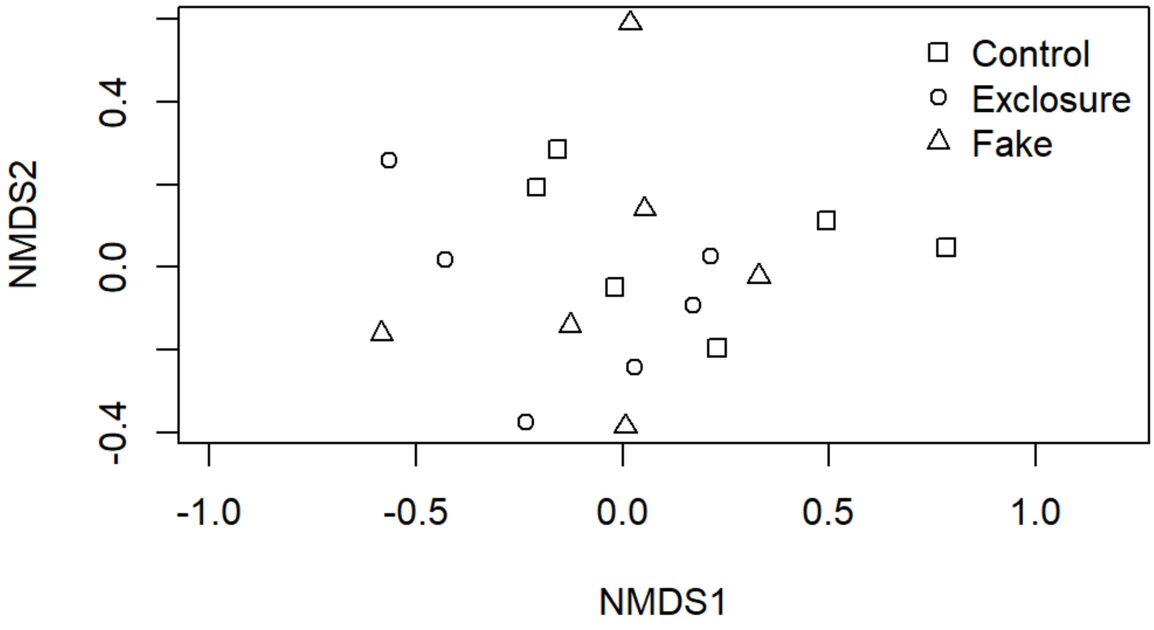

Fig. 2. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in March 1994 (stress = 0.168).

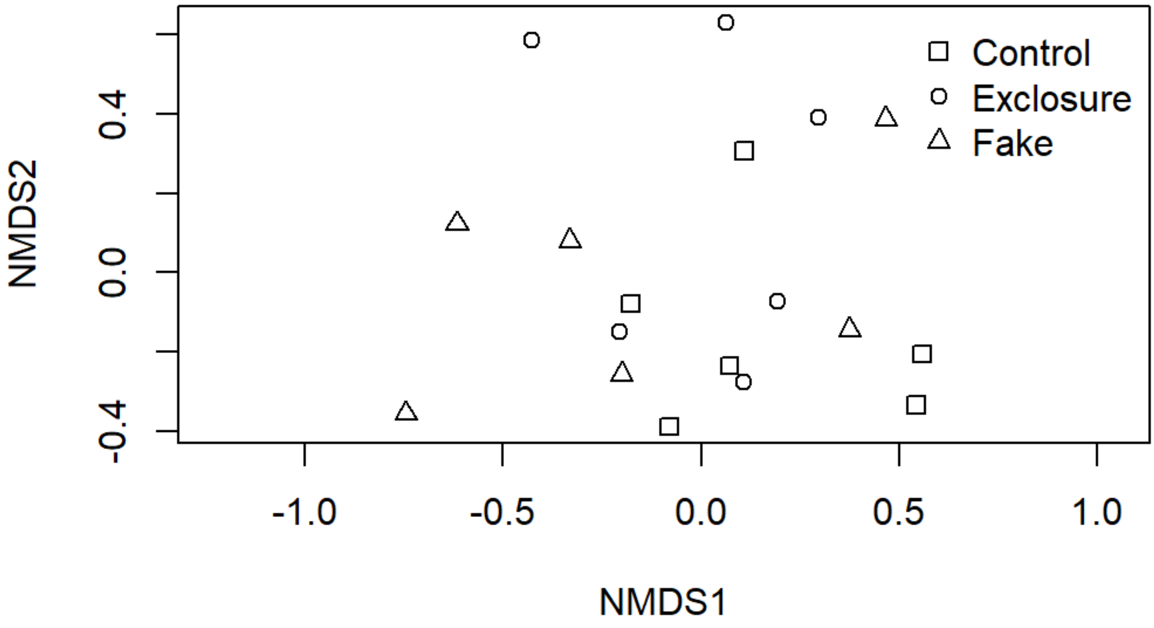

Fig. 3. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in August 1994 (stress = 0.124).

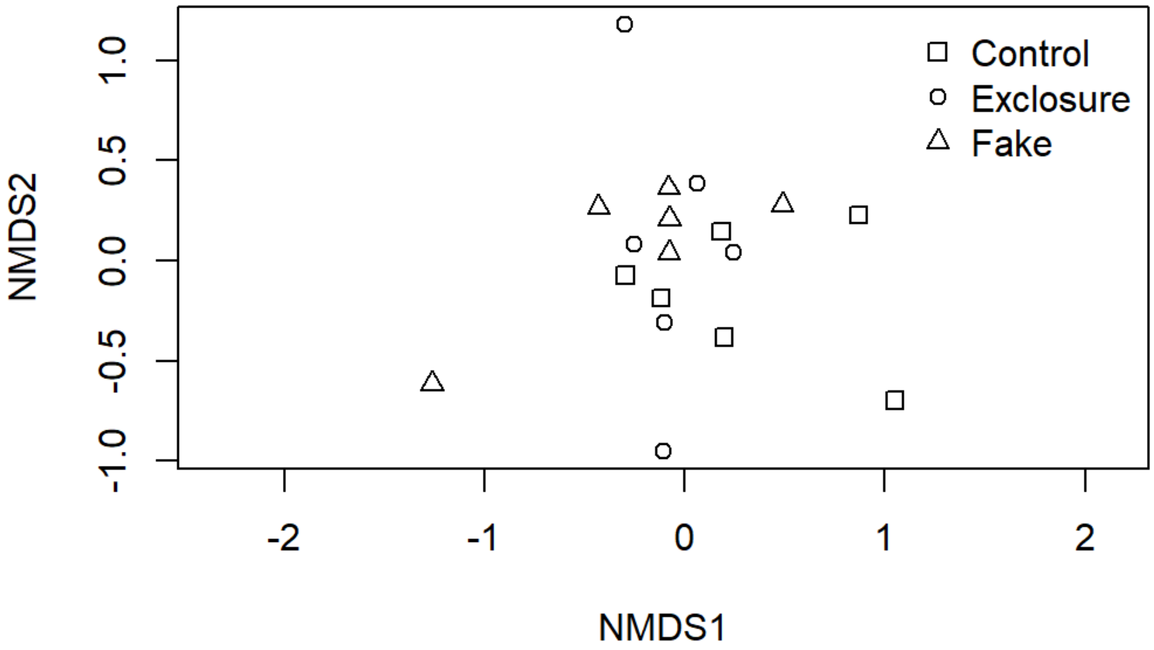

Fig. 4. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in May 1996 (stress = 0.146).

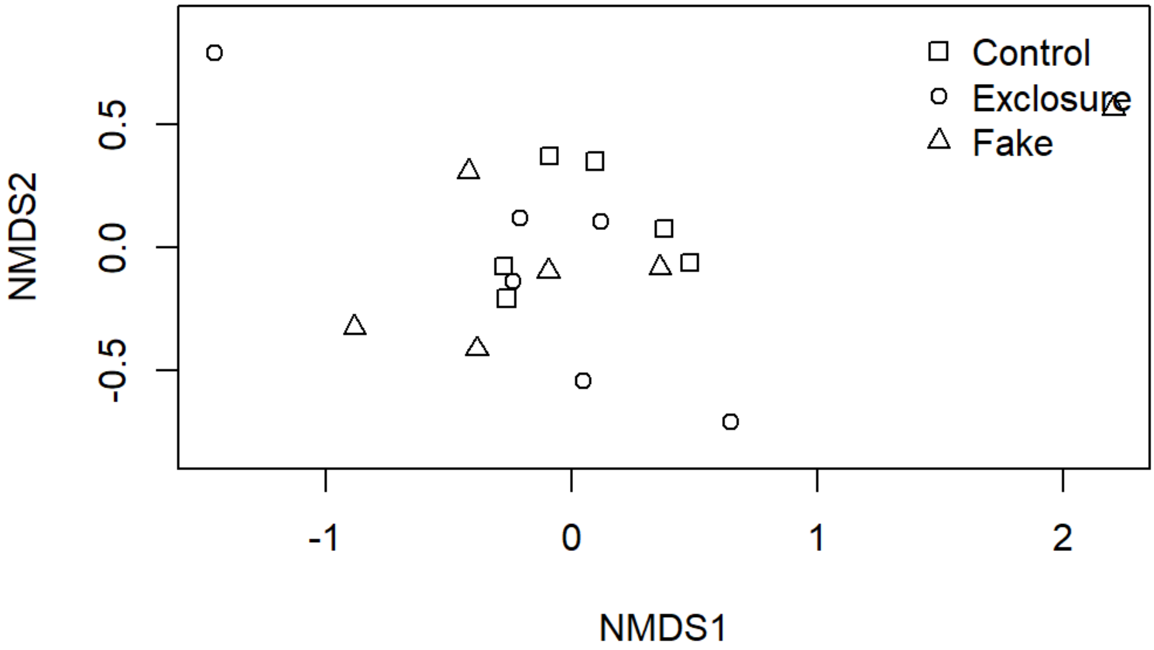

Fig. 5. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in October 1996 (stress = 0.082).

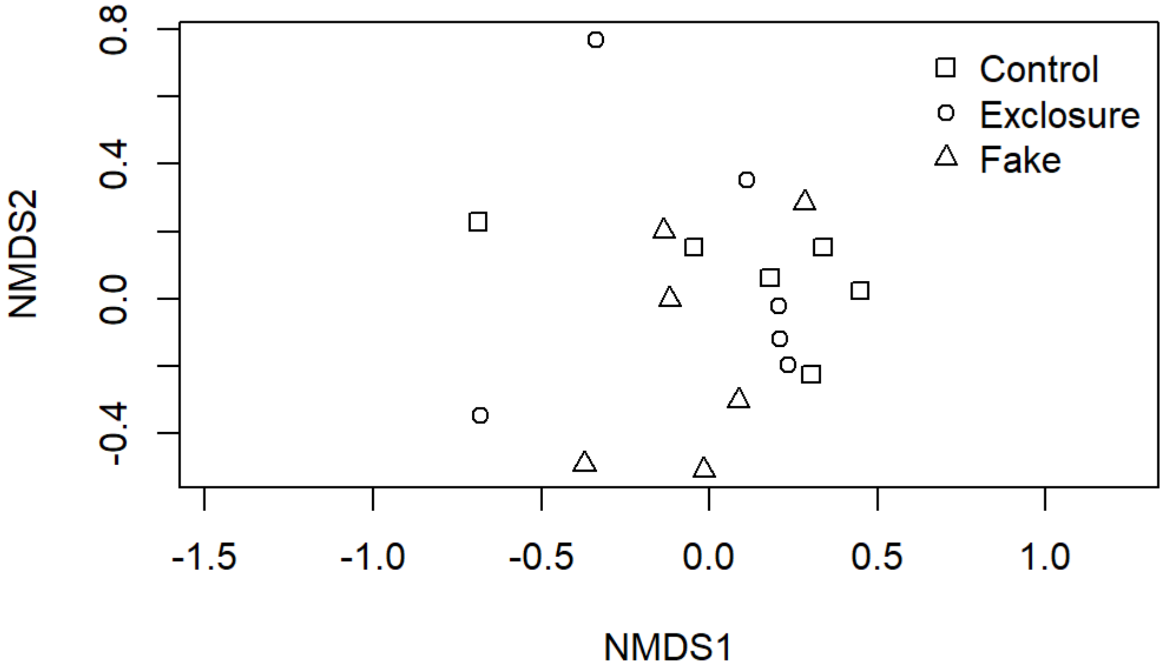

Fig. 6. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in April 1997 (stress = 0.197).

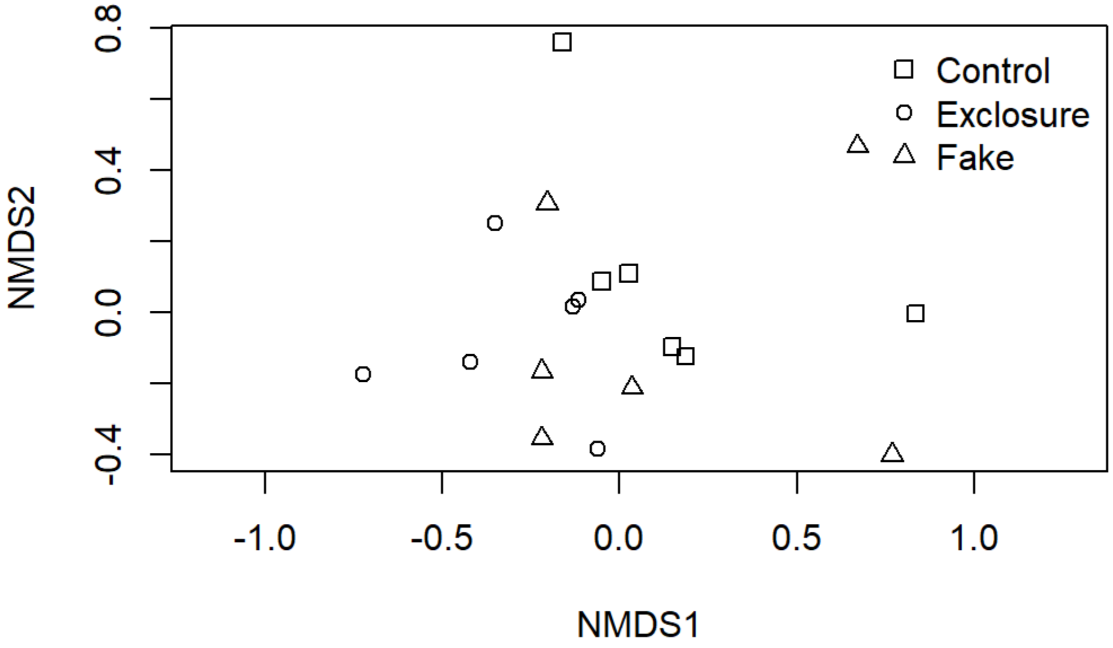

Fig. 7. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots

[fake] and open control plots [control]) from samples collected in the Simpson Desert in September 1997 (stress = 0.151).

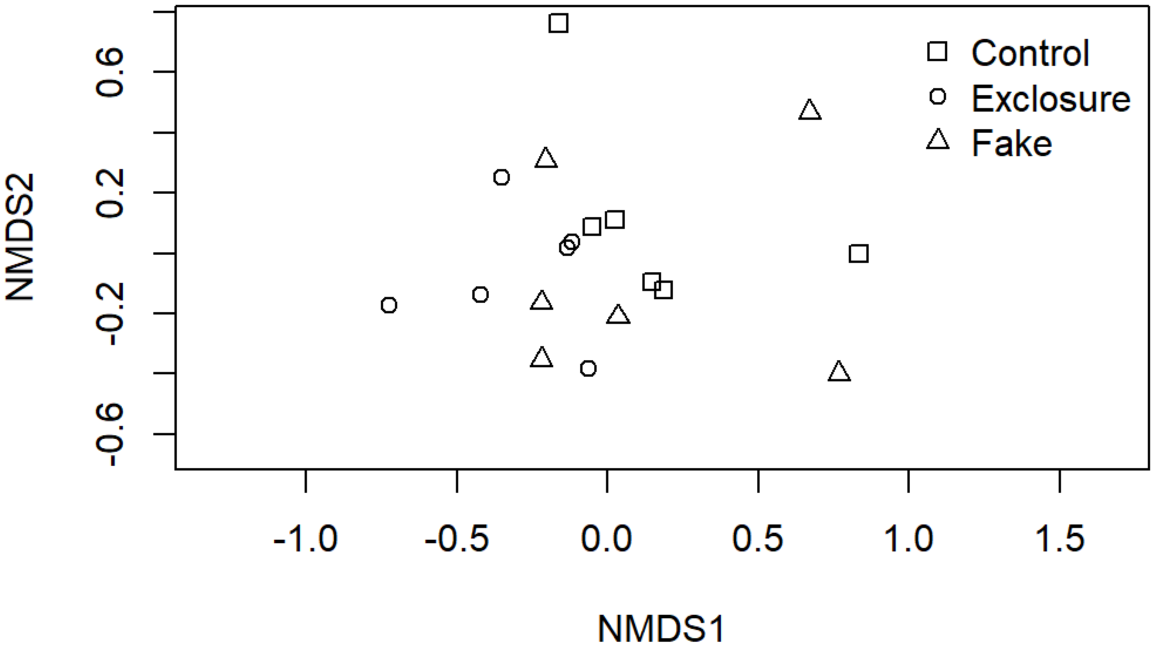

Fig. 8. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert in September 1999 (stress = 0.177).

2004-2011

The two sampling occasions in this period were carried out after heavy rainfall events, and the numbers of seeds extracted from soil samples were relatively high: 2408 from the exclosure plots, 595 from the fake-fenced plots and 546 from the open control plots (total *n* = 3549). Sixty seed species were identified. A *per*MANOVA showed that date had no effect on the seed bank (*df* = 1, *P* = 0.187), but treatment was significant (*df* = 2, *P* = 0.005). There was no date × treatment interaction (*df* = 2, *P* = 1.0).

Pairwise ADONIS comparisons showed samples from the open control and fake-fence treatments to be similar (*df* = 1, *P* = 0.989), but exclosure plot samples differed from those of the open control and fake-fenced treatments (*df* = 1, *P* = 0.001 for both the latter comparisons). An nMDS ordination of the combined 2004 and 2011 results indicated a clear separation of the exclosure seeds from those in the open control and fake-fence treatments, with considerable overlap in seed composition results for the latter two treatments (Fig. 9).

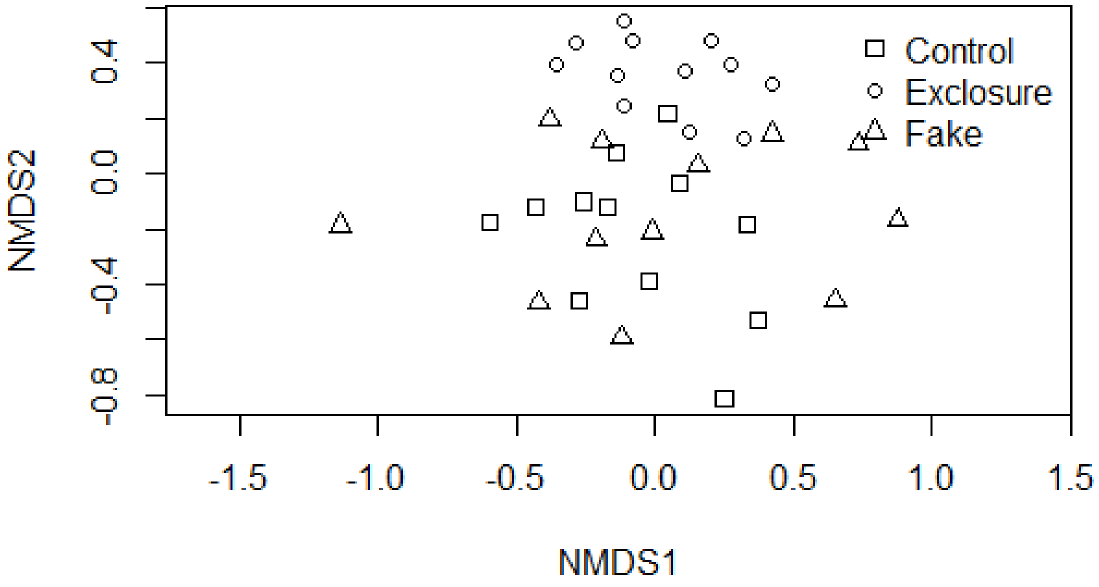

Fig. 9. Ordination by non-metric multidimensional scaling (nMDS) comparing seed species composition across three treatments (rodent exclusion plots [exclosure], fake-fenced plots [fake] and open control plots [control]) from samples collected in the Simpson Desert on two occasions, in August 2004 and October 2011 (stress = 0.146).

SIMPER identified 21 seed species that were significantly more abundant in the exclosure compared with open control treatments. In order, these were: *Grevillea stenobotrya*, *Acacia ligulata*, *Newcastelia spodiotricha*, *Crotalaria eremaea*, *Abutilon otocarpum*, *Acacia dictyophleba*, *Yakirra australiensis*, *Enchylaena tomentosa*, *Euphorbia tannensis*, *Crotalaria cunninghami*, *Acacia murrayana*, *Lechenaultia divaricata*, *Eucalyptus pachyphylla*, *Tephrosia rosea*, *Eremophila macdonnellii*, *Enneapogon polyphyllus*, *Eucalyptus gammophylla*, *Grevillea juncifolia*, *Atalaya hemiglauca*, *Petalostylis cassiodes* and *Stylobasium spathulatum*. Twenty seed species were more abundant in the exclosure than in the fake-fence treatments. In order, these were: *Grevillea stenobotrya*, *Acacia ligulata*, *Newcastelia spodiotricha*, *Cleome viscosa*, *Abutilon otocarpum*, *Acacia dictyophleba*, *Enchylaena tomentosa*, *Yakirra australiensis*, *Euphorbia tannensis*, *Crotalaria cunninghami*, *Senna pleurocarpa*, *Acacia murrayana*, *Lechenaultia divaricata*, *Eucalyptus pachyphylla*, *Eucalyptus gammophylla*, *Grevillea juncifolia*, *Atalaya hemiglauca*, *Petalostylis cassiodes*, *Stylobasium spathulatum* and *Grevillea striata*.

Discussion

The results provided strong support for the prediction that seed species composition would differ between sites where rodents had been removed compared to sites where rodents had access, but this difference took many years to become obvious. From 1994 to 1999 between 2667 and 3300 seeds from 43 plant species were counted and identified from the three experimental treatments (rodent exclosure, open control and procedural control), whereas in 2004 and 2011 60 seed species were identified and at least 4-fold more seeds were recovered from the exclosure treatment than either of the control treatments. Seeds collected during the seven sampling occasions up to 1999 differed between times and treatments, with treatment differences occurring between the open control and two other treatments, most likely due to site-specific differences in where individual plots were located. The temporal differences may have been driven by factors such as local rainfall. By contrast, seeds collected in 2004 and 2011 differed only between treatments, with the rodent exclosures having both greater numbers of seeds and more species than the open and procedural controls. Thus, differences between treatments were manifest a decade after the experimental plots had been established, and remained consistent a further seven year later. I discuss these patterns, and the drivers that may have shaped them, below.

In the first instance, it is relevant to inquire why there was no evident rodent-exclusion effect up until 1999. The effectiveness of the exclusion fences was tested and confirmed both during and between the seven sampling occasions prior to the new millennium, so the integrity of the experimental treatment was assured. However, although rodent activity was detected in the open and procedural control plots over the same time, concurrent live trapping at the study site showed that this was a prolonged period of low rodent numbers (Dickman *et al.*, 2010, 2011, 2014; Greenville *et al.*, 2016). Thus, the trapping rate of *P. hermannsburgensis* was <0.7% for much of the period between 1994 and mid-1997, and no captures of *N. alexis* (or other rodents) were made over the same period. Capture rates of both species increased briefly and only modestly after heavy but isolated rainfall events in February 2007 and April 2008 (Dickman *et al.*, 2010, 2011). The paucity of rodents was probably driven in part by food limitation, including seeds. For example, Predavec (1994) found that declines in both *P. hermannsburgensis* and *N. alexis* in 1993 after heavy rains in 1991 were correlated strongly with seed availability and that the decline in the first species could be slowed by the provision of supplementary food (Predavec, 2000). Beh (2011) reported similar results. Whatever the reasons for the limited rodent activity from 1994 to 1999 in the present study, the scarcity of rodents would have very likely contributed to their lack of impact on the seed bank.

Recovery of the seed bank after cessation of seed predation has been slow in some previous studies. Working in the Chihuahuan Desert, for example, Guo *et al*. (1995) found that changes in the seed bank and above-ground plant communities appeared three years after granivorous rodents and birds had been excluded, with the effects of bird exclusion being particularly evident. Kauffman and Maron (2006) showed that predation on bush lupine (*Lupinus arboreus*) was habitat-dependent; seed depredation occurred quickly in dune habitat but slowly and with little impact after >5 years of rodent exclusion in grassland habitat. In arid Australia, Gordon and Letnic (2016) proposed that seed predation by rodents could have previously been an important process before native rodents declined in the wake of European arrival. They showed that, at sites where a focal species—the dusky hopping-mouse *Notomys fuscus*—was common, the seeds of a common shrub were 3-fold more abundant in plots where the mice had been excluded compared with where they had access (Gordon and Letnic, 2016). Although this difference was apparent just 17 months after rodent exclusion, the authors suggested that differences in mature above-ground plants may not be manifest for years, or until large rainfall events had stimulated germination and recruitment.

In the present study granivorous birds and ants had access to all treatment plots. The removal of seeds by these taxon groups may have compensated to some degree for the lack of rodent seed predation in the fenced treatment plots. In addition, as both *P. hermannsburgensis* and *N. alexis* are not obligate granivores and consume green plant material, fungi and invertebrates as part of their overall diet (Chapter 3, Murray *et al*., 1999), the effects on the seed bank of these species, especially when occurring at low density, were unlikely to have been great and may have become manifest—if at all—only after a very prolonged period of time if conditions had remained dry.

The heavy La Niña-associated rainfall events in 2000 and 2010–2011 appear to have been catalysts for the large exclusion treatment effects that were observed in 2004 and 2011. Both events led to mass germination, recruitment and seeding by annual grasses and herbs and to later flowering and seed production by perennial shrubs and trees, as well as to large increases in consumer populations (Dickman *et al*., 2014; Greenville *et al*., 2016). These conditions effectively recharged the soil seed bank: 17 more seed species were identified in soil samples collected in 2004 and 2011 than in the seven sampling occasions between 1994 and 1999, and average numbers of seeds recovered per plot per sampling occasion in the exclusion treatment plots rose from 71.7 seeds in the period from 1994 to 1999 to 172 seeds in 2004 and 2011. Populations of *N. alexis* and *P. hermannsburgensis* erupted following the rain-stimulated pulses of food resources, achieving 10–20% rates of trap success in 2001 and rates of 40–50% in 2011 (Dickman *et al*., 2014). Although both eruptions were short-lived, lasting only several months to a year, perhaps due to influxes of avian and introduced mammalian predators (Dickman *et al*., 2014; Greenville *et al*., 2017), the elevated numbers of rodents appear to have been sufficient to reduce the abundance and species richness of seeds in the open plots where foragers had access, whereas the recharged seed banks in the rodent exclusion plots escaped predation.

Further evidence to support the idea that the treatment differences arose due to rodent predation in 2004 and 2011 is that several of the seed species that were found at higher abundances in the exclosure treatment were species that are preferred by rodents. These include the seeds of *Grevillea stenobotrya*, *G. juncifolia*, *Acacia dictyophleba*, *A. ligulata* and *N. spodiotricha* (see Chapters 3 and 6; Murray and Dickman, 1997). Notably too, many of the other seed species that were more abundant in the rodent-exclosure plots were characterized by their relatively large size (≥ 2 mm diameter), such as *Crotalaria* spp., *Eucalyptus pachyphylla*, *E. gammophylla* and *Sida fibulifera*. Although the palatability of these species is not known, all are consumed to some degree by both *P. hermannsburgensis* and *N. alexis*; large seed size is likely to equate to greater ease of handling and net rate of energy return than would be expected for small seeds (Chapter 3; McNaught, 1994; Murray and Dickman, 1994a, 1997). One surprising result was that spinifex (*Triodia basedowii*) seed was found in similar amounts across the treatments throughout the study. As spinifex seed is ostensibly preferred by rodents (Chapter 3; Murray and Dickman, 1997; Ricci, 2003), it could have been expected to accumulate in the rodent-exclusion plots. It is possible that rodents prefer fresh spinifex and that the quality of seeds recovered from soil samples was insufficient for them to be selected by rodents (see Chapter 4). Alternatively, spinifex seed may have been removed from rodent exclosures by ants or avian foragers. Further research is needed to disentangle these possibilities.

One limitation of the present study is that there were large gaps in the collection dates of samples. For example, there was a five-year gap in sampling between 1999 and 2004 and a seven-year gap between 2004 and 2011. Although I have interpreted the large rodent exclusion-treatment effect in later samples as arising due to the heavy rainfall events in 2000 and 2010–2011, it remains unclear whether the patterns described here prevailed immediately after the rains fell and whether they remained consistent for long periods. More frequent sampling may have revealed whether spinifex seed accumulated initially in the rodent-exclusion plots after it was shed, and whether other ephemeral species may have been present at times but were not detected by the irregular sampling regime. Other factors that could have influenced rodent foraging, such as the depth of leaf litter in plots (Nicolai, 2020), were not measured. A further limitation of the study is that we do not know whether seed bank differences translate into differences in the above-ground vegetation community. There is ongoing debate about the extent to which seed-predators have population-level effects on plant recruitment and community dynamics (e.g., Maron and Simms, 1997; Kauffman and Maron, 2006; Bricker *et al.*, 2010; Wang, 2020). In desert environments, where changes in the recruitment patterns of slow-growing shrubs and other perennial vegetation can take many years to become apparent (Frank *et al.*, 2013; Gordon and Letnic, 2016), very long term studies will likely be needed to uncover any effects of rodent seed predation on above-ground vegetation communities.

While the effects of rodents on soil seed banks have been well documented in many desert environments (Brown and Lieberman, 1973; Brown *et al.*, 1979; Maron and Simms, 1997), there has been little research on the effects of rodents on seed bank dynamics in arid Australia. The results from this study show that rodent seed predation does affect the soil seed bank, but suggest that in the desert system studied their effects are limited and manifest only after rainfall-induced pulse events when populations increase dramatically. During bust periods, temporal differences in the soil seed bank may be driven by local rainfall or other factors, but not by rodent predation.

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Chapter 8. General Discussion

Summary of main results

The primary aim of this thesis was to investigate the factors that influence the diet and foraging habits of Australian desert rodents, focussing in particular on the diet and foraging habits of the sandy inland mouse (*Pseudomys hermannsburgensis*). Desert rodents, particularly Australian species, have been understudied compared to their better-known North American counterparts (Watts, 1974; Murray and Dickman, 1994a; Murray *et al*., 1999); while some studies have described the diets of Australian desert rodents, research that has sought to uncover the factors that influence foraging activity, or the impacts of foraging on the environment, has been scant. This thesis hopes to go some way to filling this gap in knowledge, and represents the first in-depth study of factors that influence the diet and foraging habits of any Australian desert rodent species. It also contributes to our understanding more broadly of foraging theory and the ecology of rodents in Australian desert environments.

In the sections below, I describe the main results of the study and conclude by reviewing the implications of my work for understanding the diet and foraging behaviour of desert rodents, in particular *P. hermannsburgensis*. Some of the challenges and opportunities for future research are also discussed.

Key findings of the study

Foraging and seed selection in rodents: the diet of the sandy inland mouse Pseudomys hermannsburgensis

Early studies on the diet of the sandy inland mouse indicated that the species was probably granivorous, although sample sizes were often too small to be conclusive (Watts, 1970, 1972; Morton, 1979; Watts and Morton, 1983). In 1994, Murray and Dickman agreed that seeds were a major component of the diet of *P. hermannsburgensis*, but argued that the strong and consistent presence of invertebrates and green plant material was more indicative of omnivory than granivory. The results in this study support those of Murray and Dickman

(1994a), confirming that seeds are an important food category in the diet of *P. hermannsburgensis* and also that invertebrates and green plant material are frequently consumed. Thus *P. hermannsburgensis* is more accurately classified as an omnivore than as a granivore. Direct observations showed that animals foraged almost entirely on the soil surface, but would make shallow digs to locate buried food. Analysis of stomach contents showed a significant dietary shift with respect to invertebrate prey: there was an increased presence of invertebrates in the diet during bust compared to boom periods in the environment. This dietary shift was considered likely to represent a survival strategy by *P. hermannsburgensis*, with invertebrates partly replacing seeds in the diet during the prolonged bust periods when seeds are scarce.

Foraging and seed selection of rodents under different risks of predation

Direct observations indicated that *P. hermannsburgensis* appear to be vigilant and are easily disturbed when foraging, suggesting that they may be aware of the risk of predation. Using cafeteria-style experiments, mice were shown to select and consume larger quantities of preferred seeds in sheltered than in risky, open microhabitats when predators were active, but consumed their preferred seeds similarly in both microhabitats when predator activity was low. A temporal switch in seed preference was also observed, from *Triodia basedowii* seed to that of *Grevillea stenobotrya*. The results suggested that *P. hermannsburgensis* balances the dual imperatives of avoiding predation risk and selecting its preferred (and presumably higher quality) foods while foraging, and that the perception of predation risk is finely adapted to the activity of its main mammalian predators.

Foraging and seed selection in rodents: influence of moisture and seed burial depth

Although animals observed while foraging seldom appeared to dig for food, experimental burial of a preferred seed species—*Grevillea stenobotrya*—showed that *P. hermannsburgensis* could detect and excavate seeds buried at depths of 5 cm in the soil. However, depth was a significant factor in seed retrieval by *P. hermannsburgensis*, with seeds taken mostly from the soil surface and at the shallow depth of 0.5 cm; fewer seeds were taken at burial depths of 1.5 cm, 3.0 cm and 5.0 cm. The strong inverse relationship between seed burial depth with seed detection and consumption presumably indicates that the food reward at depth does not outweigh the energy and time expenditure and the increased risk of predation that are associated with deep excavations. Surprisingly, hydrating the seeds did not significantly affect the retrieval/consumption of seeds by *P. hermannsburgensis*; seeds were consumed at the same rate regardless of being dry or moistened. This result was surprising as it contrasts with previous findings that moist seeds are more attractive (or more detectable) to desert rodents (Johnson & Jorgensen, 1981; Vander Wall, 1993; Taraborelli *et al.*, 2009). Nonetheless, it is clear that *P. hermannsburgensis* has acute olfactory detection, and it is possible that the ability to detect buried seeds in dry soil using olfactory cues is an important adaptation for persistence in frequently dry desert environments.

Foraging and seed selection in rodents: effects of seed familiarity

A body of theoretical work suggests that foragers should focus on familiar, commonly-encountered food types when foraging because these foods can be recognized and handled more quickly and predictably than rarely-encountered food types (Kelrick *et al.*, 1986; Kotler & Brown, 1988; Murray & Dickman, 1994b). Cafeteria-style seed choice experiments in sites with contrasting seed banks provided some support for theoretical expectations, but only in one of two years when experiments were run. In the second year, there was no evident food-familiarity effect, and mice instead selected two seed species—*Acacia dictyophleba* and *Grevillea stenobotrya*—that they probably found to provide high net energetic returns. It was speculated that familiar seeds may be taken to minimise the time spent foraging when environmental conditions are not limiting, thus allowing more time for activities such as reproduction, but when *per capita* food or water resources are constrained animals will focus their foraging on food types that minimise the risk of starvation.

Impacts of rodents on the soil seed bank

Rodents were shown to have an effect on the soil seed bank in the Simpson Desert, but the effect of excluding rodents became evident only after heavy rainfall events triggered pulses of primary productivity and eruptions of rodents. During a prolonged dry period (1994–1999) rodents were scarce and had little evident impact on the soil seed bank. Following heavy rainfall events in 2000 and 2010–2011 the soil seed bank was recharged and rodent populations erupted; sampling then showed seeds in rodent exclusion plots to be more abundant and more diverse than in control plots. The results suggested that rodents have little effect on the soil seed bank for long periods when conditions are dry and rodent numbers are low, but can have large effects on the soil seed bank during the brief periods when their populations are elevated post-rain. The results also provide quantitative support for prior speculation that temporal variation in desert soil seed banks is linked to rainfall (Greenville *et al*., 2012, 2017).

Implications and further considerations

Seed preferences

Much of the work in this thesis was predicated on the expectation that seeds are an important part of the diet of *P. hermannsburgensis* and that, in consequence, mice would be selective in where they forage and in respect of which seeds they consume. Early results (Chapter 3) confirmed that seeds are indeed an important dietary component for *P. hermannsburgensis* and suggested that spinifex (*Triodia basedowii*) seed was likely to be a preferred seed species. These observations also supported previous research. Murray and Dickman (1997) identified spinifex as the most consumed seed species in their first cafeteria trial, and Ricci (2003) found that spinifex seed was important in triggering reproductive activity in both spinifex hopping-mice (*Notomys alexis*) and *P. hermannsburgensis*. Two of the earlier cafeteria trials, as indicated in Chapter 4, further supported the suggestion that spinifex is a highly preferable seed, but subsequent cafeteria trials, as described in Chapter 4 and Chapter 6, found that spinifex was not selected to the extent that would be expected of a preferred seed species. These observations suggest that foragers' preferences for particular foods are not immutable: either the food preferences of foragers change, or the quality of their food varies. With respect to the observed switch in preference by mice for spinifex seed, the latter possibility is most likely. Murray and Dickman (1997) and Ricci (2003) used fresh spinifex seed in their trials, and these seeds had markedly higher water contents than the seeds I used here, especially in my later experiments when only dry seed was available. In addition, fresh green seed contains higher levels of essential amino acids than dry seed, and this appears to determine the preference of granivorous birds such as zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*) for fresh seed (Allen and Hume, 1997). Although I did not assay seeds for micronutrients, seeds such as *Grevillea stenobotrya* and *Acacia* *dictyophleba* had relatively high energy or water contents, and this may have made them more profitable for consumption by *P. hermannsburgensis*.

In almost all the cafeteria trials I performed, *G. stenobotrya* emerged as a highly selected seed. By contrast, Murray and Dickman (1997) found *P. hermannsburgensis* to consume greater amounts of spinifex and *Sida physocalyx* seeds than those of *G. stenobotrya* in their cafeteria trials. The seeds of *S. physocalyx* in those trials had a higher water content than those of *G. stenobotrya*, perhaps contributing to their preference by mice. Relatively high seed water content may also explain why the seeds of *A. dictyophleba* were highly selected as shown in Chapter 6 and why this species was one of the three most highly consumed seed species, out of 10 species that were offered, in the cafeteria trials of Murray and Dickman (1997). However, seed water content offers only a partial explanation for seed preference by *P. hermannsburgensis*. *Trachymene glaucifolia* seed was not highly consumed in the experiments reported in Chapter 4 despite having the highest water content of the seeds that were offered.

Overall, the inconsistent results from cafeteria trials found in the current study and in comparison with the results of Murray and Dickman (1997) suggest that many different factors influence seed preference by *P. hermannsburgensis*. In addition to intrinsic qualities such as seed energy and water content, palatability, age, size, shape, micronutrients, the presence of a hard seed coat or protective spines (Murray and Dickman, 1994a,b), contextual factors such as predation risk and the familiarity and accessibility (e.g., buried or not) of seeds to foragers may all affect seed preference. The multitude of factors that influence seed preference by rodents is likely to make it difficult to obtain consistent results in cafeteria-style trials, especially when these are carried out in the field (Kotler and Brown, 1988). Future experiments could consider assaying key seed qualities such as mass, energy and water content immediately before seeds are used in trials, and could also manipulate moisture content by drying or soaking seeds to achieve desired differences. However, this approach would require well-equipped field facilities; these were not available in the present study.

A further imperative that may influence seed consumption, and could help to explain the consumption of ostensibly preferred and non-preferred seed species by rodents, is that multiple different food sources could be needed to ensure acquisition of particular minerals, micronutrients or other chemicals to ensure growth and wellbeing. The importance of micronutrients for plant growth, animal growth and nutrition is generally well known (Broadley *et al*., 2012; Upadhaya and Kim, 2020), even if there is little or no information on the needs for such resources specifically by desert rodents. The results in Chapters 4 and 6 showed that *P. hermannsburgensis* generally ate small amounts of most or all seeds that were offered, even if they generally consumed more of certain species than others. Murray and Dickman (1997) suggested that such 'partial sampling' could be important for rodents such as *P. hermannsburgensis* and spinifex hopping-mice (*Notomys alexis*) to identify which foods to focus on when faced with different options; the results of the present study support this possibility. The findings of Chapter 5 and work by others (e.g., Frank, 1988a,b; Vander Wall, 1993; Vander Wall *et al*., 2003) indicate that olfaction would most likely be used to determine subtle differences in water content or other aspects of seed quality, but sampling small amounts of different seeds could potentially help to confirm a decision about whether to continue consuming those seeds.

Boom and bust

A major influence on the diet of *P. hermannsburgensis*, and probably other desert-dwelling rodents, is the boom and bust nature of the environment they inhabit. During prolonged dry periods mice are likely to face food shortages, including a reduction in the abundance and diversity of seeds (Chapter 7), but their ability to forage widely and exploit open microhabitats may be increased because dry periods are usually characterized by low predator activity (Pavey *et al*., 2008; Dickman *et al*., 2014; Greenville *et al*., 2014). Indeed, in Chapter 4 it was shown that mice utilized sheltered microhabitats to selectively consume preferred seeds when predation risk was high, whereas open microhabitats were exploited to obtain preferred seeds during dry periods when predation risk was low. Animals use other strategies to obtain sufficient food during bust periods, such moving long distances to exploit ephemeral food resources (Dickman *et al*., 1995; Letnic, 2002), and may rely more on olfaction to detect seeds (and possibly other food types) that are buried in dry sand (Chapter 5). The ability of *P. hermannsburgensis* to change its diet was shown in Chapter 3, where more invertebrates were recorded in the stomachs of *P. hermannsburgensis* during bust periods than during booms. Because bust periods may continue for several years there should be strong selective benefits to mice that can find sufficient food to grow and reproduce; delaying reproduction until the 'good times' arrive is not likely to be a viable strategy for animals that have a life expectancy of perhaps 1–2 years (Breed, 1990; Breed and Ford, 2007; Jackson *et al*., 2023).

Heavy rainfall, especially if it occurs over summer, stimulates rapid germination of annual grasses and herbs as well as growth and reproduction of perennial plant species. This provides an almost immediate resource pulse for consumers, as well as a longer-lasting pulse as rainfall has the effect of recharging the soil seed bank (Chapter 7). When resources are abundant *P. hermannsburgensis* may include relatively greater amounts of familiar, common or preferred foods in its diet (Chapter 6), thereby minimizing the time spent foraging and maximizing the time available for social and reproductive activities. In support of this, Dickman *et al*. (2010) showed that both *P. hermannsburgensis* and spinifex hopping-mice increase their burrow fidelity after rain and aggregate in greater numbers than during bust times, providing conditions conducive to breeding. However, such social changes are usually short-lived, with diet being constrained by the increased risk of predation as mobile predators move into arid areas post rain (Pavey *et al*., 2008; Greenville *et al*., 2014).

As well as the effects of the boom and bust cycle on rodents, the findings of Chapter 7 suggested that rodents may also affect the trajectory of the seed bank—and potentially long-term vegetation dynamics—by selectively consuming certain seeds more than others when their numbers are high in the boom and post-boom period. The results of Chapter 7 were driven primarily by just two species, *P. hermannsburgensis* and *Notomys alexis*, as these species comprised >95% of all rodent captures in concurrent live-trapping during the 17-year period over which the seed bank was sampled (Dickman *et al*., 2014; Greenville *et al*., 2016). Eruptions of long-haired rats (*Rattus villosissimus*) occurred just before and just after the seed bank sampling (Predavec and Dickman, 1994; Greenville *et al*., 2013), thus precluding this species from having any evident effect on the results. If sampling had been extended in time, potentially stronger effects may been evident on the seed bank. Similarly, if other species that had at one time occurred in the arid regions before declining or becoming extinct (e.g., shorttailed hopping-mouse, *Notomys amplus*; long-tailed hopping-mouse, *N. longicaudatus*; mainland populations of Gould's mouse, *Pseudomys gouldii*) erupted to high numbers after heavy rains, the combined impact of many seed-eaters on the seed bank could have been potentially quite pervasive. Gordon and Letnic (2016) proposed that the functional extinction of desert rodents in arid Australia had led to dramatic changes in the seed bank, and to marked shifts in the structure and composition of above-ground vegetation; my results provide additional support for this proposal, but also indicate that future work should monitor both seed bank and vegetation dynamics in rodent exclusion experiments.

Future research

The experiments in this thesis were completed over a relatively short period of time and mostly during bust times when productivity and overall animal numbers were low. It would be of considerable interest to carry out the same experiments during a boom phase when food and other resources are abundant. Unfortunately, boom periods are difficult to predict and plan for, and logistical problems would likely be encountered at experimental sites in separating the foraging decisions of multiple species that erupt during booms (Dickman *et al*., 2010; Letnic and Dickman, 2010). However, as boom periods, with their temporarily large populations of rodents, appear to reset the desert seed bank, research on the diets, foraging decisions and foraging impacts of rodents would be of great value at these times. As my experiments were carried out also during seasonally-constrained times—for example, no cafeteria experiments were carried out in summer—further research across all seasons could be considered. Hot, dry summer conditions may result in mice placing a higher premium on consuming foods with a higher moisture content, as appears to be the case for small dasyurid marsupials that select 'juicier' invertebrates during dry, but not wet, conditions (Baker and Dickman, 2018). Long-term monitoring would be needed to explore such effects, and should also attempt to quantify above-ground vegetation dynamics and the potentially different impacts of different rodent species.

The focus of this thesis was on *P. hermannsburgensis* because it was the most common and most reliably present species of rodent. However, spinifex hopping-mice also are relatively common, and species such as the desert mouse (*Pseudomys desertor*) and the long-haired rat can occur temporarily in higher numbers after heavy rainfall events in the study region. *P.hermannsburgensis* occurs in other arid habitats dominated by chenopod shrubs, Mitchell grass and tropical-arid savannas (e.g., Breed and Ford, 2007; Kutt *et al*., 2004), as do several other species of native rodents (Watts and Aslin, 1981; Breed and Ford, 2007; Jackson *et al*., 2023), but none has yet been subject to any detailed studies of their foraging ecology.

Other areas not investigated in this thesis relate to the characteristics of different food types that affect consumption by rodents. For example, Murray and Dickman (1994b) found that both *P. hermannsburgensis* and *N. alexis* preferred invertebrates (mealworm larvae, *Tenebrio molitor*) when given the choice to consume these, or fungal material or the seeds and stems of spinifex (*Triodia basedowii*), and Chapter 3 showed that the former species consumed more invertebrates during bust periods than during booms. Comparing the relative availability of different types of food is notoriously difficult (Manly *et al*., 2002), and disentangling the intrinsic (food quality) and extrinsic (environmental) factors that influence diet choice still more so, and perhaps represents one of the next frontiers in the field of foraging ecology (Calver and Loneragan, 2023). With respect to seeds alone, a multiplicity of factors may interact to influence what is eaten. Energy and water content are likely to be fundamentally important, but essential nutrients, lipids, amino acids, minerals and other chemicals may be needed in trace amounts or at certain life stages by consumers. In future experiments it would be of value to assay as many of these essential nutrients as possible in seeds and to offer a large range of choices to different rodent species to gain more insight into what foragers seek when choosing different foods. A further useful metric to understand why certain seeds, or other foods, are preferred, would be the net intake rate of that food when foraging. Although energy is the standard currency of foraging models, the above discussion suggests that energy is only one of several currencies that foragers may employ. Net rates of intake of energy or other components of food are difficult to estimate in rodents in the field, but could be much more practicable under controlled conditions in captivity (Jackson *et al*., 2023).

Conservation and management implications

There has been a severe reduction in the richness of native Australian rodent species, in some arid areas to just 44% of the levels that prevailed pre-European settlement (Morton and Baynes, 1985). At least 11 species have become extinct on mainland Australia, six species are critically endangered and many more species are becoming locally vulnerable or endangered. An extensive list of possible reasons for these declines has been proposed, including changes in fire regimes from the reduction or cessation of traditional Aboriginal fire management practices, long periods of drought combined with the clearing of drought refuges, and the introduction of non-native species such as rabbits, cattle, house mice and especially predators such as European red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) (Woinarski *et al*., 2015; Gordon and Letnic, 2016; Lavery *et al*., 2022). While *P. hermannsburgensis* remains common and is not facing imminent extinction, it has declined and is regionally vulnerable in New South Wales and southern parts of Western Australia (Dickman, 1993).

It is easy to dismiss a species that is considered common as being of any kind of conservation concern, but species such as the blue-grey mouse (*Pseudomys glaucus*), Gould's mouse (*P. gouldii*) and several arid-dwelling *Notomys* species were probably also relatively common less than two centuries ago (Woinarski *et al*., 2014, 2015). In the case of *P. hermannsburgensis*, numbers decline quickly and dramatically from the peaks that are achieved during rain-triggered eruptions; the declines are driven in part by diminishing food resources (Predavec, 1994; Beh, 2011), but also by increased *per capita* predation from predators such as the feral cat and red fox (Dickman *et al.*, 1999, 2010; Greenville *et al*., 2013). At low numbers, populations are at risk of further decline or local extinction due to continuing predation, events such as wildfire, prolonged drought, or stochastic events such as the inability to find mates (Breed and Ford, 2007; Jacob, 2008; Greenville *et al*., 2014).

The loss of a species, even locally, represents not just a reduction of species diversity but also a potential impact on the species' ecosystem. Local extinction of *P. hermannsburgensis* could have various flow-on consequences. In Chapter 7 *P. hermannsburgensis* and *N. alexis* were together shown to affect the abundance and richness of seeds in the seed bank; if these rodents selectively feed on large seed species, such as those of many shrubs, their loss could lead ultimately to increased shrub cover (see Gordon and Letnic, 2016). Rodents, including *P. hermannsburgensis*, have also been suggested to suppress the growth of spinifex through seed consumption, potentially influencing the dispersion and cover of spinifex hummocks and thus the suitability of open vs sheltered microhabitats used by reptiles (Pianka, 1986; Dickman, 1999). *P. hermannsburgensis* is also an important prey item for both native and feral predators, including goannas (*Varanus* spp.), birds of prey, feral cats and the European red fox (Dickman, 1996; Mahon, 1999; Kutt *et al*., 2020). If there were a local loss of *P. hermannsburgensis*, predators would likely switch to hunting other species and in turn increase pressure on alternative, potentially scarce, prey. During population booms of the long-haired rat, for example, rats form the major prey of the feral cat but as the rat population declines during the bust phase cats switch their diets to other species of rodents and place extra predation pressure on other prey groups such as birds and reptiles (Yip *et al*., 2014, 2015). *P. hermannsburgensis* also creates burrows for shelter and reproduction that are often used as permanent or temporary shelters by other species such as dasyurid marsupials, reptiles and frogs; if *P. hermannsburgensis* were to disappear, many of these refuges would not be available (Dunlop and Pound, 1981; Dickman, 1996; Breed and Ford, 2007).

To develop appropriate conservation strategies for any at-risk species, we must have reliable information about the species' habitat needs, diet and foraging behaviour, and which threats are most important to the species' survival (Breed and Ford, 2007; Jacob, 2008; Woinarski *et al*., 2014). This thesis has focused primarily on the sandy inland mouse (*Pseudomys hermannsburgensis*), and provides a more detailed understanding of the foods the species consumes and the factors that influence when, where and how foraging takes place. It is likely to be at its most vulnerable during prolonged busts when populations are low and resource abundance and diversity are least; these are the times when management could most effectively intervene to recover numbers in local areas. It is not certain how transferrable the information of one species may be to others, but at the least such information should help to inform approaches to research on related species that are cryptic or endangered and difficult to study. Possible dietary analogues for *P. hermannsburgensis* may be the desert-dwelling plains mouse (*Pseudomys australis*; IUCN-vulnerable, Burbidge and Woinarski, 2016) and the recently reclassified Gould's mouse (*P. gouldii*; Roycroft *et al*., 2021).

Conclusions

‘Basic knowledge of the species ecology is necessary when developing a conservation strategy’ (Breed and Ford, 2007). As previously discussed in the introduction, the diets and foraging behaviour of Australian desert rodents have been largely unexplored, especially in comparison with the better-known heteromyids and other rodents in the American deserts. The overall outcome of the research conducted in this thesis is that considerably more information has been uncovered about the diet and foraging habits of the sandy inland mouse (*Pseudomys hermannsburgensis*), and more general insights have been obtained also on some of the predictions of foraging theory. By focusing on *P. hermannsburgensis* I had hoped to develop a model that could be used and expanded to focus subsequent research on the resource requirements of other desert rodents. Overall, my results have revealed that the diet and foraging habits of *P. hermannsburgensis* are influenced by complex and varied suites of factors that differ between times and probably places, and that in turn the mice exert influence on their food resources, most notably on seeds in the soil seed bank. As noted above, knowledge of animals' resource needs and how these needs are met is important for conservation, even for species such as *P. hermannsburgensis* that are considered, currently, to be at little risk of future extinction.

While this thesis focuses on *P. hermannsburgensis*, I hope that the knowledge gained from my research provides broader insight into the foraging habits and preferences of Australian desert rodents, and that the information presented here might act as a catalyst to stimulate and guide future research on a wide range of other species.

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