

# The role of refuges in the persistence of Australian dryland mammals

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## ABSTRACT

Irruptive population dynamics are characteristic of a wide range of fauna in the world's arid (dryland) regions. Recent evidence indicates that regional persistence of irruptive species, particularly small mammals, during the extensive dry periods of unpredictable length that occur between resource pulses in drylands occurs as a result of the presence of refuge habitats or refuge patches into which populations contract during dry (bust) periods. These small dry-period populations act as a source of animals when recolonisation of the surrounding habitat occurs during and after subsequent resource pulses (booms). The refuges used by irruptive dryland fauna differ in temporal and spatial scale from the refugia to which species contract in response to changing climate. Refuges of dryland fauna operate over timescales of months and years, whereas refugia operate on timescales of millennia over which evolutionary divergence may occur. Protection and management of refuge patches and refuge habitats should be a priority for the conservation of dryland-dwelling fauna. This urgency is driven by recognition that disturbance to refuges can lead to the extinction of local populations and, if disturbance is widespread, entire species. Despite the apparent significance of dryland refuges for conservation management, these sites remain poorly understood ecologically. Here, we synthesise available information on the refuges of dryland-dwelling fauna, using Australian mammals as a case study to provide focus, and document a research agenda for increasing this knowledge base. We develop a typology of refuges that recognises two main types of refuge: fixed and shifting. We outline a suite of models of fixed refuges on the basis of stability in occupancy between and within successive bust phases of population cycles. To illustrate the breadth of refuge types we provide case studies of refuge use in three species of dryland mammal: plains mouse (*Pseudomys australis*), central rock-rat (*Zyzomys pedunculatus*), and spinifex hopping-mouse (*Notomys alexis*). We suggest that future research should focus on understanding the species-specific nature of refuge use and the spatial ecology of refuges with a focus on connectivity and potential metapopulation dynamics. Assessing refuge quality and understanding the threats to high-quality refuge patches and habitat should also be a priority. To facilitate this understanding we develop a three-step methodology for determining species-specific refuge location and habitat attributes. This review is necessarily focussed on dryland mammals in continental Australia where most refuge-based research has been undertaken. The applicability of the refuge concept and the importance of refuges for dryland fauna conservation elsewhere in the world should be investigated. We predict that refuge-using mammals will be widespread particularly among dryland areas with unpredictable rainfall patterns.

*Key words:* refugia, mammal, rodent, dasyurid marsupial, irruptive dynamics, arid, dryland.

## CONTENTS

I. Introduction .....	648
II. Use of the term 'refuge' in the literature .....	649
(1) Concepts of refuge .....	649

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(2) Refuge <i>versus</i> refugium .....	650
III. Definitions and typology of refuges .....	650
(1) Previous definitions .....	650
(2) Definition of refuge used by irruptive mammals .....	650
(3) Refuge typology .....	651
(a) Shifting refuge .....	651
(b) Fixed refuge .....	651
IV. Case studies of refuge use .....	651
(1) Plains mouse, <i>Pseudomys australis</i> .....	651
(a) Species characteristics .....	651
(b) Habitat preferences .....	653
(c) Refuge use and type .....	653
(d) Drivers of population and occupancy dynamics .....	653
(e) Persistence in refuges .....	654
(2) Central rock-rat, <i>Zyomys pedunculatus</i> .....	654
(a) Species characteristics .....	654
(b) Habitat preferences .....	654
(c) Refuge use and type .....	654
(d) Drivers of population and occupancy dynamics .....	654
(e) Persistence in refuges .....	655
(3) Spinifex hopping-mouse, <i>Notomys alexis</i> .....	655
(a) Species characteristics .....	655
(b) Habitat preferences .....	656
(c) Refuge use and type .....	656
(d) Drivers of population and occupancy dynamics .....	656
(e) Persistence in refuges .....	657
(4) Other refuge-using species .....	657
V. Methodology for refuge location .....	658
VI. Potential threats .....	659
VII. Future research agenda .....	660
VIII. Conclusions .....	661
IX. Acknowledgements .....	661
X. References .....	661

## I. INTRODUCTION

Arid or dryland environments comprise just over 37% of the world's land mass (Warner, 2004) with much of this area characterised by unpredictable precipitation patterns. This unpredictable precipitation produces unpredictability in cycles of resource availability which in turn have profound impacts on dryland biota (Ostfeld & Keesing, 2000; Yang *et al.*, 2008, 2010). As a consequence, a significant component of dryland-dwelling fauna is characterised by irruptive population dynamics, with population abundance tracking changes in the availability of key resources (Jaksic *et al.*, 1997; Letnic & Dickman, 2010; Meserve *et al.*, 2011). Irruptive population dynamics are driven by periods of high precipitation that lead to increased germination and growth of ephemeral, annual and perennial plant species (Ostfeld & Keesing, 2000). These pulses in primary productivity result in increases in both reproduction and survivorship of folivorous, granivorous and omnivorous fauna and lead to population irruptions in these species after time lags of several months to a year (Previtali *et al.*, 2009; Letnic & Dickman, 2010; Shenbrot, 2014).

Irruptive population dynamics are characteristic of a wide range of dryland-dwelling fauna (e.g. Yang *et al.*, 2008;

Atkinson *et al.*, 2014) and may arise in several ways. For example, periods of prolonged precipitation may break dormancy in animals with resting stages in their life history (e.g. many invertebrates; Crawford, 1981) or elevate the metabolic rates of animals that are aestivating (e.g. burrowing frogs; Hillman *et al.*, 2009), in turn providing opportunities for population growth *via in situ* reproduction. By contrast, more-mobile fauna such as birds may move into dryland areas following heavy precipitation events, achieving irruptions over local or regional areas initially by immigration and then by reproduction (Dean, 2004). Other animals may irrupt if widespread precipitation events improve conditions over large regional areas, allowing them to move from discrete refuge sites into the broader dryland environment (Newsome & Corbett, 1975; Morton, 1990). This latter strategy has perhaps been used most often to explain the irruptive dynamics of dryland mammals (Letnic & Dickman, 2010; Pavey *et al.*, 2014b), although many other taxa with local dispersal abilities appear to exhibit similar dynamical patterns.

Among mammals, population irruptions are best known among rodents in many of the world's drylands (e.g. Newsome & Corbett, 1975; Fichet-Calvet *et al.*, 1999). Other dryland mammal groups that undergo irruptive

dynamics include some lagomorphs, eulipotyphlans (e.g. Chung-MacCoubrey, Bateman & Finch, 2009) and several orders of marsupials (Dasyuromorphia, Didelphimorphia, Diprotodontia) (e.g. Dickman *et al.*, 2001; Lima *et al.*, 2001). Population irruptions of mammals and other vertebrates are often referred to as ‘booms’ or ‘ratadas’.

Recent attention has focussed on the mechanisms by which irruptive species, particularly small mammals, are able to persist during the extensive dry periods of unpredictable length that occur between resource pulses in drylands. These periods are of considerable importance as resource pulses may occur as infrequently as once per decade. In the western Simpson Desert of central Australia, for example, it is estimated that the low (or bust) phase of mammal population cycles occupies 8.5 out of every 10 years (Pavey *et al.*, 2014a). In this region, as well as the drylands of southern Africa, India and South America where prolonged dry periods are punctuated by occasional high-precipitation events, many species drop to low population abundance or become locally extinct during these dry periods (Griffin, 1990; Tripathi, 2005; Moseby *et al.*, 2006). However, recolonisation occurs after heavy precipitation and the subsequent resource pulse, and the pattern of occurrence of a given species within the landscape is often one of local extinction and recolonisation events (Milstead *et al.*, 2007; Dickman *et al.*, 2011).

There is growing evidence that regional persistence of small mammal populations occurs as a result of the presence of refuge habitats or refuge patches into which populations contract during dry periods (Milstead *et al.*, 2007; Letnic & Dickman, 2010; Greenville, Wardle & Dickman, 2013; Pavey *et al.*, 2014a). These refuge areas act as a source of animals when recolonisation occurs during and after subsequent resource pulses (Naumov, 1975; Brandle & Moseby, 1999; Dickman *et al.*, 2011). Such refuge areas appear to occupy only a small portion of the landscape that is occupied during population outbreaks. For example, refuge habitats for the rodents *Oligoryzomys longicaudatus* and *Abrothrix longipilis* in north-central Chile occupied only about 2% of the study area (Milstead *et al.*, 2007). The term refuge is hereafter used to refer to these refuge habitats and patches, with drought used interchangeably with bust and low phase of population cycles.

Protection and management of refuges is increasingly recognised as a priority for the conservation of dryland-dwelling mammals and other fauna (Letnic & Dickman, 2010; Pavey *et al.*, 2014a). There is growing evidence that disturbance to refuges can lead to the extinction even of species that are abundant during population outbreaks (e.g. see Lockwood & DeBrey, 1990). In dryland Australia, for example, refuges can experience high levels of predation from introduced predators, such as the feral cat (*Felis catus*) and red fox (*Vulpes vulpes*), because they represent significant concentrations of biomass in a dry and resource-poor environment (Pavey *et al.*, 2014a). In dryland regions generally, refuge habitat is threatened by a range of other disturbances including farming, pastoralism and tourism (Bahre, 1979; Ayyad & Ghabbour, 1986; Seely & Pallett, 2008).

Despite the likely significance of refuges for the persistence of dryland fauna, there are few published empirical data on their characteristics or locations. Also of concern is that the term refuge is used frequently in the literature but is often not defined, or is poorly defined, and there is regular conflation between the terms ‘refuge’ and ‘refugium’ (e.g. Nekola, 1999; Davis *et al.*, 2013). With these shortcomings in mind, herein we aim to synthesise available scientific information on the refuges of dryland-dwelling fauna, using Australian mammals as a case study to provide focus, and to document a research agenda for increasing this knowledge base.

We begin this review by examining the use of the terms ‘refuge’ and ‘refugium’ in the literature and setting the refuges used by dryland fauna within this terminology. Next we provide a definition of, and develop a typology of, refuges. We then present three case studies of dryland-dwelling mammal species that illustrate the breadth of refuge types used and the variability in the level of ecological understanding across species.

We next present a three-step approach to locating refuges. The inclusion of a methodology section is driven by the lack of available information on refuge location and usage and the knowledge that all published descriptions of refuge habitats and/or patches indicate that these comprise a small proportion of the landscapes that they occupy (Brandle & Moseby, 1999; Milstead *et al.*, 2007; Pavey *et al.*, 2014a). Next, we assess potential threats faced by the different refuge types and consider how present-day refuge location may be influenced by the actions of threatening processes such as introduced predators in the recent past. Thus we consider the possibility that refuges may now be located in relatively threat-free habitats or habitat patches. We conclude this review by developing an ongoing research agenda for refuges. This agenda details the information that is needed to further our understanding of these important features of drylands.

## II. USE OF THE TERM ‘REFUGE’ IN THE LITERATURE

### (1) Concepts of refuge

The term ‘refuge’ is widely used in biology, but the term encompasses a range of divergent phenomena (Berryman & Hawkins, 2006). Various concepts based on the term are used in theories of ecology, biogeography, evolution and speciation. However, in many cases the term refuge is used erroneously when actually referring to refugia/refugium (see Section II.2 for clarification on the distinction of the two concepts).

In ecology, the term ‘refuge’ refers to the life history of species and how individuals within a population are able to survive despite the presence of predators and parasites (e.g. Elton, 1939). This view has been developed further within the discipline of population ecology so that refuge is an important aspect of predator–prey population dynamics (Berryman & Hawkins, 2006; Owen-Smith, 2008). The concept is also widely applied in insect pest management. In

recent years, refuge has been applied in conservation science with potential refuges being important sites in conservation planning and in decision-science approaches. The term is also in common conservation parlance where it is sometimes used to denote areas that are legally protected from anthropogenic disturbance, especially hunting (Keppel *et al.*, 2012).

## (2) Refuge versus refugium

The term ‘refuge’ is often used interchangeably with ‘refugium’ (or its plural ‘refugia’) in the literature (Keppel *et al.*, 2012). This conflation has created confusion about what each term refers to and is exacerbated by various definitions which mix process, pattern and mechanisms when defining and applying these terms. Several recent reviews have recognised these issues and sought to separate the two concepts.

A unifying feature in separating the two terms is that refugia are seen to operate at broader temporal and/or spatial scales than refuges. Specifically, a refuge is seen to operate over timescales of minutes to decades. By contrast, refugia operate on longer timescales of millennia (Keppel *et al.*, 2012). This separation of the two terms on the basis of time and the understanding that speciation in many taxa occurs over time frames of >100000 years (Lister, 2004) also enables a separation of the two concepts on the basis of the evolutionary processes that may operate. Therefore, refugia are locations where organisms can adapt to changing conditions in order to persist over time. Davis *et al.* (2013) extended these ideas to develop the complementary terms of ecological refuge and evolutionary refugia and went on to apply the terminology to aquatic habitats in arid Australia. Aquatic habitats with the greatest degree of decoupling of microclimate from regional climate were the most likely to function as evolutionary refugia (Davis *et al.*, 2013).

Keppel *et al.* (2012) developed a definition of refugia as sites to which organisms retreat, persist in and potentially expand from under changing environmental conditions. As indicated above, refugia have been identified as sites where the local climate is decoupled from the regional climate (Dobrowski, 2011) and, therefore, sites where a species can persist if the regional climate changes in an unfavourable direction. Thus the term refugia should be used when referring to range dynamics and climate change (Keppel *et al.*, 2012; Mackey *et al.*, 2012).

## III. DEFINITIONS AND TYPOLOGY OF REFUGES

### (1) Previous definitions

Refuges have been variously defined, but definitions have been poorly tested, are not scaled, or mix processes and patterns. For example, Morton & Baynes (1985) defined refuges as places where animal species can persist through drought owing to the existence of relatively dependable supplies of moisture and nutrients. Such a definition conflicts

with those that emphasise structural elements that minimise predation risk (e.g. Morton *et al.*, 1995; Burbidge & Manly, 2002) or provide relief from fire effects (e.g. McDonald *et al.*, 2013). Definitions have largely precluded considerations of species-specific requirements (i.e. autecology), making it difficult to identify potential refuge-using species.

Some recent usage defines refuges at very fine spatial and temporal scales that are applicable to individual animals. Under this concept, a refuge is a location where an individual can escape from difficult circumstances, particularly predation, such as under a rock, into a burrow or an area of dense vegetation (e.g. Li *et al.*, 2014). Den sites, where an animal rests for the day or night or where it aestivates or hibernates, are also considered to be refuges. In the context of fire, refuges are defined as habitat features within a landscape that in the short term facilitate the survival or persistence of organisms in the face of a fire event that would otherwise result in their mortality, displacement or local population extinction (Robinson *et al.*, 2013).

### (2) Definition of refuge used by irruptive mammals

Here we develop a definition of refuge that is based on Keppel *et al.*'s (2012) approach to defining and classifying refugia. Specifically, the approach involves a process-based definition, centred on species-specific requirements in a multidimensional domain of environmental variables, space and time. In the temporal dimension, we consider that refuges operate on timescales of decades or less. In the spatial dimension we consider that a refuge must be of sufficient area to support a local population of a species. Thus we do not consider refuges at the scale of the individual. Specifically, refuges are not only sites that provide protection from predation (see Berryman & Hawkins, 2006) but also enable a local population to persist.

We recognise that species with irruptive population dynamics are likely to be obligate refuge users, with the use of refuges between population irruptions analogous to species distributional changes over much longer timescales, such as during glacial cycles. These species are considered to be obligate refuge users because populations outside refuges during dry periods are expected to go extinct in a similar manner to populations outside refugia during times of climate change (Stewart *et al.*, 2010).

We define a refuge as a subset of the potential range of a species with irruptive population dynamics where a viable population persists during the low phase of the population cycle (i.e. the bust phase). We refer to a species with irruptive population dynamics as an irruptive species. An irruptive species is one that experiences population outbreaks that result in significant increases in both the area of occupancy and population size before contracting back to spatially restricted areas with specific habitat attributes.

In all documented cases, irruptions have been triggered by a pulse in primary productivity. Such pulses are often driven by precipitation but can also be driven by food moving in from outside the range of the irruptive species (e.g. desert locusts; Atkinson *et al.*, 2014).



### (3) Refuge typology

Below we present a typology of refuge types. The aim is not to present a taxonomy of refuges but rather to show the variation that is currently understood in refuge types and to illustrate that refuges can have different temporal and spatial dynamics. As the refuge concept is more widely tested in the future it is probable that other refuge models will become apparent.

We recognise two main types of refuge: a shifting refuge and a fixed refuge. In addition, four potential types of fixed refuge are recognised. A shifting refuge has a set of intrinsic properties that make it more suitable than the surrounding landscape for limited periods of time (typically at a scale of weeks or months) for any one particular species. A fixed refuge has a set of intrinsic properties that make it consistently more suitable (typically on a scale of years or decades) than the surrounding landscape for any one particular species. Models of shifting and fixed refuges are given in Fig. 1 and are expanded upon below.

#### (a) Shifting refuge

Refuges are most commonly assumed to occur in fixed or predictable locations. In drylands, however, where moisture is critically important for life, refuges may shift from place to place over short time periods depending on the spatial variability of precipitation (Fig. 1, model 1). A species that exploits shifting refuges uses a large number of small and highly localised refuges, moving from one to another in rapid succession. In introducing the concept of shifting refuges, Newsome & Corbett (1975) recognised that these could be exploited only by animals that are both able to track ephemeral flushes of resources, as they are created by local precipitation events, and have the ability to access them by directed movement. Mobile organisms such as birds could be expected to exploit such spatially and temporally variable resources most effectively (e.g. Tischler, Dickman & Wardle, 2013), although Newsome & Corbett (1975) argued that some species of rodents could disperse sufficiently long distances to exploit temporary resource patches. This was confirmed by Dickman, Predavec & Downey (1995), who showed that three species of rodents and three species of dasyurid marsupials increased their movements during or just after rainfall, with most movements (74%) being directed to where rain had recently fallen.

#### (b) Fixed refuge

Fixed refuges are those that occur in predictable locations and that are used consistently over time. We describe four models of fixed refuge use. These differ on the basis of whether the species' use of the refuges is stable between and/or within busts (Fig. 1, models 2A–D). A species that uses fixed refuges that are stable between busts uses the same refuge patches across consecutive bust periods and also typically continues to occupy the same refuges during the intervening boom phase. A species that uses fixed refuges

that are unstable between busts uses a different set of refuge patches from one bust period to the next bust period. Some of the refuge patches may be the same across busts, but not all. A species that uses fixed refuges that are stable within a bust occupies each of the refuge patches for the duration of the bust period, while a species with fixed refuges that are unstable within a bust period uses one or more of the refuge patches for only part of a bust period.

Based on these criteria, the four models of irruptive species usage of fixed refuges (Fig. 1, models 2A–D) are those that are: (A) stable within and between busts (model 2A); (B) unstable within busts and stable between busts (model 2B); (C) stable within busts and unstable between busts (model 2C); (D) unstable within and between busts (model 2D). Note that models 2A and 2B are based on the use of specific refuge patches (i.e. refuges are stable between busts), whereas models 2C and 2D rely on the importance of broad refuge habitat rather than patches (i.e. refuges change between busts).

The stability criteria for fixed refuge models (A) and (C) defined above do not preclude the possibility that individuals move from one occupied refuge to another within a bust. However, the movement of individuals is predicted to be bi-directional and a population continues to occupy each fixed refuge patch. If such movement does occur, then the refuges in a local area may function as a meta-population.

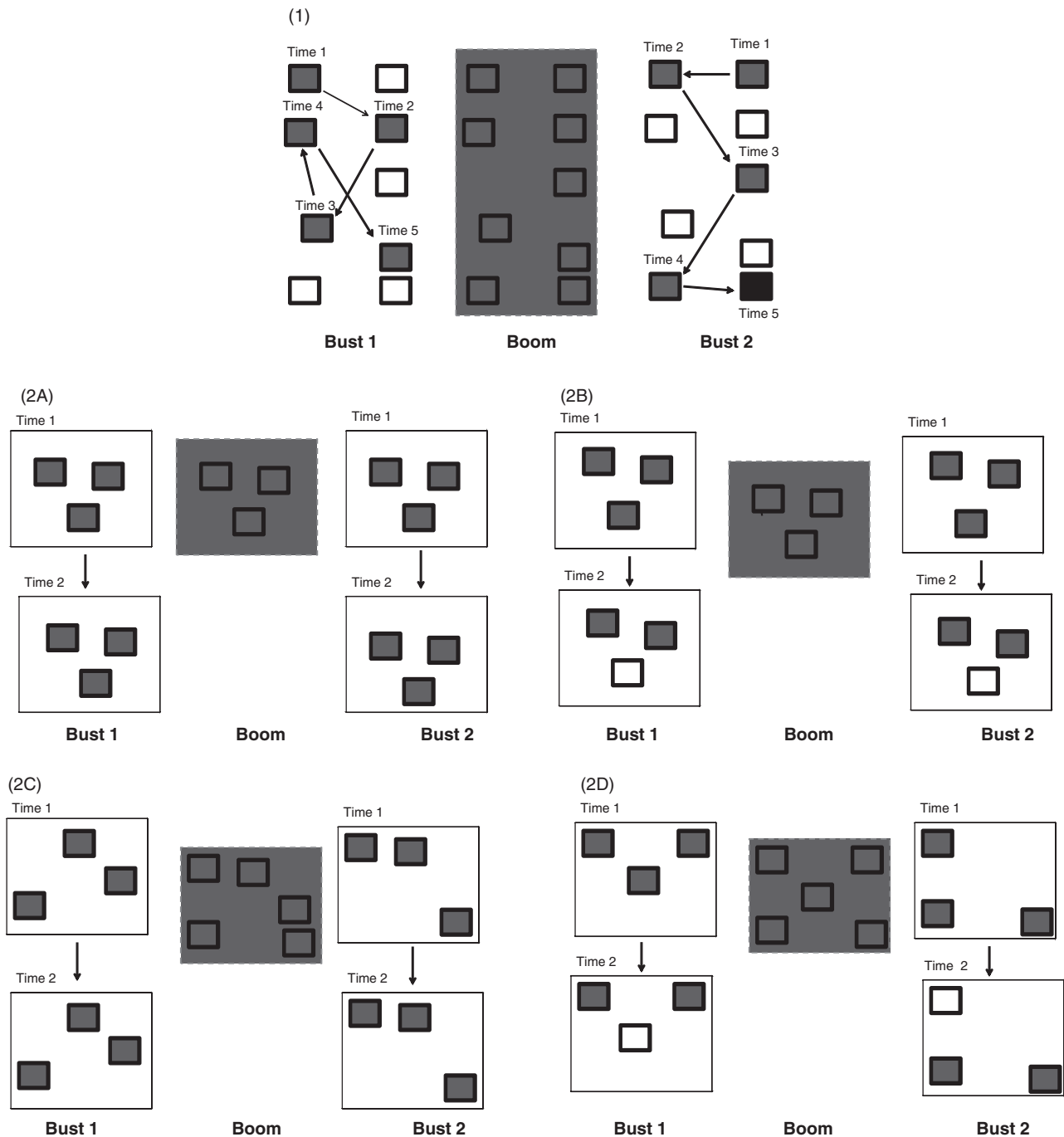
## IV. CASE STUDIES OF REFUGE USE

Below we present three case studies of refuge use in small mammals. These species were chosen because of the significant amount of information available and the range of refuge types that they represent.

### (1) Plains mouse, *Pseudomys australis*

#### (a) Species characteristics

The plains mouse (*Pseudomys australis*) is a rodent (Muridae) (body mass 30–65 g) endemic to a 700 km north–south band of stony desert habitat and interdunal plains within the Simpson and Strzelecki Deserts, Australia (Brandle, Moseby & Adams, 1999). It is listed globally as Vulnerable (Woinarski, Burbidge & Harrison, 2014). Females have four nipples, can suckle up to four young and may produce successive litters every 2–3 months (Breed, 1990), thus enabling an irruptive population response to increased resource abundance. Dramatic increases in abundance and area of occupancy have been documented in response to rare, large-magnitude climate-driven resource pulses (Brandle & Moseby, 1999; Pavey *et al.*, 2014a). Plains mouse populations and area of occupancy are large while resource availability remains high, but fall rapidly as resources decline (Brandle & Moseby, 1999; Pavey, Eldridge & Heywood, 2008a). Brandle & Moseby (1999) detected an 80-fold decrease in estimated population size during their 3-year



**Fig. 1.** Models of refuge types showing changes in the pattern of occupancy of an irruptive mammal species across boom and bust cycles. Boxes represent refuges. Shaded areas are occupied by the irruptive species, unshaded areas are not occupied. Movement of individuals from one refuge to another within busts is expected to occur for the fixed refuges and is not indicated in the diagrams. Model 1 is for shifting refuges; models 2A–D are for fixed refuges: 2A, stable within and between busts; 2B, unstable within busts and stable between busts; 2C, stable within and unstable between busts; 2D, unstable within and between busts.

study of this species within a favoured habitat patch. The area of occupancy during busts declined to 17% of the boom areas in the western Simpson Desert (Pavey *et al.*, 2014a). The range of habitats occupied is greater during population outbreaks than during the low phase of the cycle (Pavey & Nano, 2013).

(b) *Habitat preferences*

The plains mouse occurs primarily on cracking clay and gibber plains within stony desert. Occurrence is often associated with areas receiving moisture from the surrounding landscape (hereafter referred to as 'run-on' areas) and minor drainage features, but not with areas receiving large water flows and prolonged ponding such as major drainage channels, floodplains and swamps (Brandle *et al.*, 1999). Friable cracking clay soils supporting little or no perennial vegetation are characteristic of the preferred habitat (Brandle *et al.*, 1999).

(c) *Refuge use and type*

Run-on patches within stony desert are considered to be refuge habitat for the plains mouse (Brandle & Moseby, 1999; Pavey *et al.*, 2014a). Minor localised rainfall events that produce limited run-off provide moisture to these run-on patches which then produce flushes of grasses and forbs. This vegetation is an important food resource for the plains mouse (Brandle & Moseby, 1999; Pavey *et al.*, 2014a).

The occurrence of plains mouse refuges is associated with topographic position and soil type, which are fixed in the landscape and unlikely to change substantially over ecological timeframes, except where significant landscape modification occurs through accelerated erosion or deposition. Plains mouse refuges therefore fit the fixed refuge concept (see Fig. 1, models 2A–D). There is evidence that the species' use of refuges fits both model 2A – fixed refuges with stability in refuges within and between busts (R. Brandle, unpublished data) – and model 2B – fixed refuges with instability in refuge location within busts but stability between busts (Pavey *et al.*, 2014a; C. R. Pavey, unpublished data). Empirical support for the species fitting model 2B comes from populations in both South Australia and the Northern Territory. Specifically, a regularly sampled refuge in northern South Australia was occupied for 2 years during the early phase of a bust in 1993–1995 and then had no animals during the remainder of the sampling period (Brandle & Moseby, 1999). Plains mice in a study area in the western Simpson Desert, Northern Territory, used a series of four fixed refuges from 2007 to 2014. One of these was occupied for only part of a bust (from October 2007 to March 2009) and then abandoned (Pavey *et al.*, 2014a). The other refuges were occupied during the two bust phases and the intervening boom (C. R. Pavey, unpublished data). Individually marked plains mice in this study were recorded moving between refuges during a bust phase (C. R. Pavey, unpublished data).

(d) *Drivers of population and occupancy dynamics*

The primary driver of population increase in the plains mouse is precipitation. Rainfall triggers primary productivity and the subsequent increase in food availability drives reproduction (Brandle & Moseby, 1999). In captivity, plains mice will continue to breed throughout the year and a gestation period of 30–35 days gives the species the capacity for a rapid increase in population size (Smith, Watts & Crichton, 1972). Such reproduction appears to occur only during times of high resource availability in the wild (Watts & Aslin, 1981).

In plains mouse habitat in the western Simpson Desert, summer bias in rainfall is more marked in high-precipitation years and it typically occurs as discrete, short pulses of 5–6 weeks duration. This summer bias in rainfall favours extensive plant growth (Nano & Pavey, 2013). Increased food availability likely increases plains mouse reproductive activity and survivorship, leading to increases in population density and eventual dispersal from refuges. A summer rainfall event of 75 mm led to significant breeding and a within-refuge population increase of the species, but did not produce a population outbreak. By comparison, summer rainfall events of >100 mm do produce population irruptions (Pavey *et al.*, 2014a), with the species moving into a range of habitats not occupied during dry periods (Pavey & Nano, 2013). Populations of plains mouse show marked increases 4–9 months after heavy summer rain (Pavey & Nano, 2013) with dispersing individuals appearing outside of refuge habitat within 4 months (C. R. Pavey, unpublished data).

The rate of population increase is likely to be slowed by declining food resources and increased levels of predation from mammalian carnivores [dingo (*Canis dingo*), feral cat, red fox] and native birds of prey [eastern barn owl (*Tyto javanica*), southern boobook (*Ninox novaeseelandiae*), letter-winged kite (*Elanus scriptus*) (Pavey *et al.*, 2008a; Pavey, Gorman & Heywood, 2008b; McDonald & Pavey, 2014)]. Predation may also contribute to dramatic post-resource pulse population declines. The impact of predation by mammalian carnivores may be further increased in the presence of the European rabbit (*Oryctolagus cuniculus*) as this species supports high predator densities.

Other potential drivers of plains mouse population dynamics may be important. Disease may act to cause declines at high population densities when individuals are stressed as resources become depleted. High levels of use of refuge habitat by livestock [cattle (*Bos taurus*), sheep (*Ovis aries*)] and other ungulates [feral horse (*Equus caballus*), feral one-humped camel (*Camelus dromedarius*)] may impact refuges and reduce the size of refuge populations, thus muting the response to resource pulses. The combination of grazing and trampling removes ground cover and seed sources, and can also damage burrows. Finally, competition for food and shelter may be a factor, especially from the larger, native, long-haired rat (*Rattus villosissimus*) which invaded plains mouse habitat during a resource pulse in 2010–2011 (Pavey & Nano, 2013).

*(e) Persistence in refuges*

Some refuges appear to be occupied for the entire duration of the bust phase of the population cycle. Pavey *et al.* (2014a) recorded capture rates in refuges during the low phase of the population cycle equal to or higher than those in outbreak sites during the population peak, indicating that these refuges are important for the persistence of the plains mouse during dry periods. Refuge populations remain in good condition and plains mice continue to breed in refuges throughout the dry period (Brandle & Moseby, 1999; Pavey *et al.*, 2014a). By contrast, populations outside refuges appear to go extinct during dry periods. A number of key resources are present in refuges that enable persistence of the plains mouse. Shelter is present in the form of protected burrow systems (dug in sandy soil under shrubs) and deep soil cracks (that provide protection from predators and environmental extremes). Food is available as a result of the landscape characteristics of these areas that enable a regular supply of green food and seed accumulation.

**(2) Central rock-rat, *Zyzomys pedunculatus****(a) Species characteristics*

The central rock-rat (*Zyzomys pedunculatus*) is a medium-sized (body mass 70–150 g) rodent (Muridae) endemic to mountain ranges and adjacent foothills in central Australia. The species is listed globally as Endangered, with a recommendation that this be upgraded to Critically Endangered as it is undergoing declines and is little known (Woinarski *et al.*, 2014). In captivity, central rock-rats live to a maximum of 7 years and breed between the ages of 2 and 5 years. Females can produce multiple litters during a year and show the capacity to breed year-round, with young recorded in all months except June and September. Average litter size is three. This reproductive capacity means that the species can respond to periods of resource abundance by rapidly increasing in population size. Dramatic increases in abundance and area of occupancy have been documented in response to a large-magnitude climate-driven resource pulse (Edwards, 2013b).

*(b) Habitat preferences*

The species was recorded from several mountain range systems in central Australia until 1960 but then remained undetected until 1996 when it was rediscovered in a remote part of the mountainous MacDonnell Ranges (Nano, 2008). Over the following 7 years the central rock-rat was recorded at 13 sites across a 600 km<sup>2</sup> area of the West MacDonnell National Park (NP) and a nearby cattle station (Nano, 2008). In this period the species was recorded from tussock and hummock grasslands and tall open shrublands on a range of rocky substrates (Nano, 2008). It underwent a population irruption in 2000–2001. In 2002, when drought conditions prevailed and wildfires burnt a large proportion of the region (Turner, Ostendorf & Lewis, 2008), central rock-rats disappeared from monitoring sites near Ormiston Gorge

and the species has not been captured there since (Edwards, 2013a). Targeted surveys in 2009–2010 located an extant population near the summit of Mt Sonder (at 1380 m above sea level), and the species has since been recorded from a further two locations in the West MacDonnell NP and at a single location 70 km west of there (McDonald *et al.*, 2013, 2015a; Fig. 2). All these recent locations are on high-elevation (>1100 m) quartzite ridges and mountain peaks, despite substantial survey effort at lower elevations and on other geologies throughout the region (McDonald *et al.*, 2013). This landform type is now considered core refuge habitat (McDonald *et al.*, 2013, 2015a). Vegetation on these landforms is characterised by a ground layer dominated by either hummock grasses or a mixture of forbs and sub-shrubs with the upper strata comprised of scattered low shrubs or mallee-form eucalypts.

*(c) Refuge use and type*

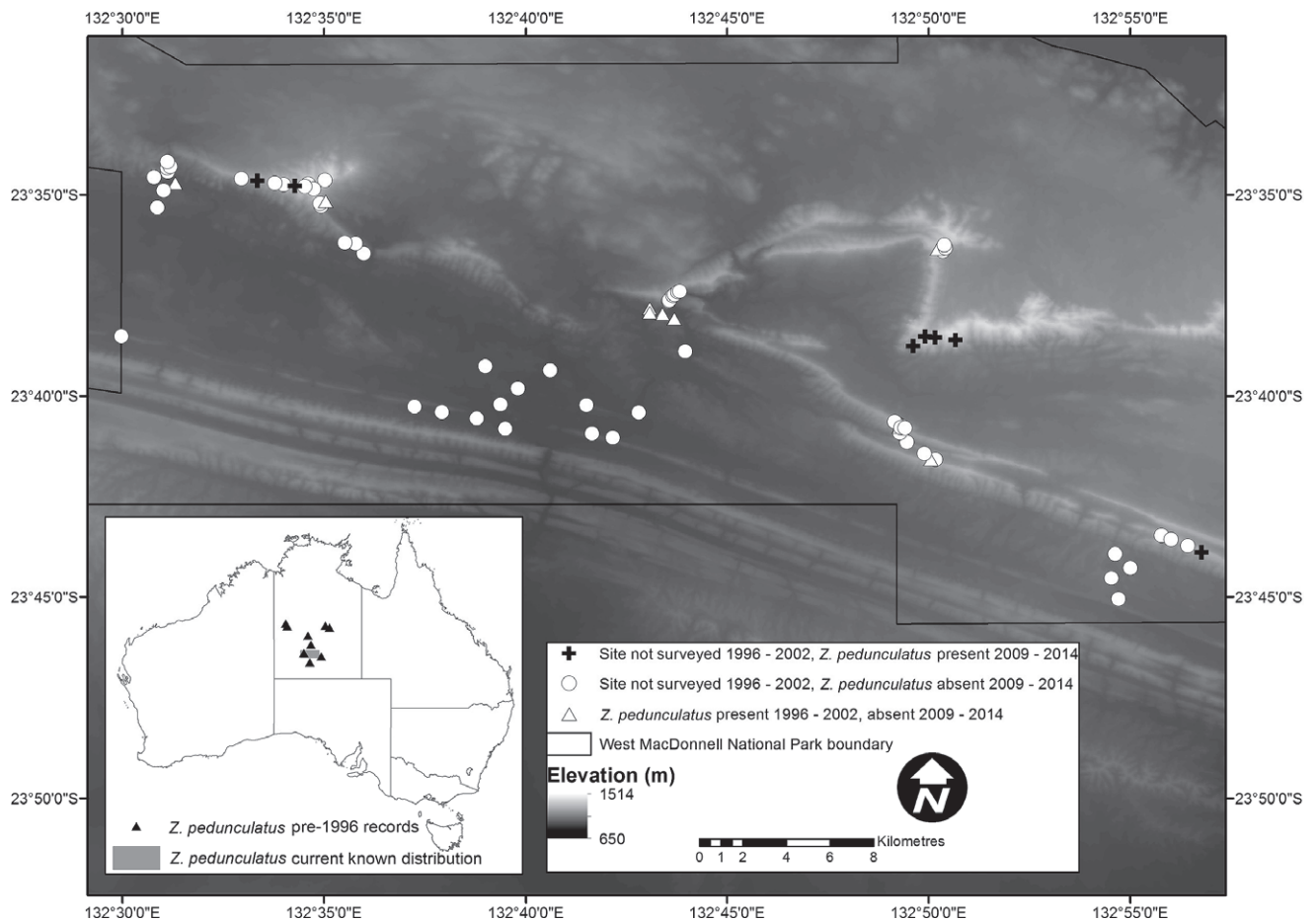
High-elevation quartzite ridges and mountain peaks are considered to be core refuge habitat of the central rock-rat. The factors defining the refuge quality of this habitat are poorly understood, although protection from both predation by feral cats and disturbance from wildfires have been suggested as hypotheses (McDonald *et al.*, 2013, 2015b). Recent research on Australian small mammals shows that declines in population size after fire occur as a result of fire-induced loss in vegetation cover which increases the vulnerability of individuals to predation; that is, individuals survive the fire but are subsequently depredated in the more open habitat (Körtner, Pavey & Geiser, 2007; McGregor *et al.*, 2014). The tendency for wildfire extent to be patchy on high-elevation ridges and peaks in the MacDonnell Ranges may contribute to these acting as refuges, particularly from feral cat predation. Food resources are not thought to be a major limiting factor as the central rock-rat feeds on the seeds and stems of a range of widespread grass, forb and shrub species, including many that are fire-encouraged (Nano, Smith & Jefferys, 2003; Edwards, 2013b).

The occurrence of refuges of the central rock-rat is strongly associated with topographic position. These quartzite ridges and mountain peaks are fixed in the landscape and will not change over ecological timeframes. Central rock-rat refuges therefore fit the fixed refuge concept (Fig. 1, models 2A–D). The available information suggests that the species' use of refuges fits model 2A – fixed refuge with stability in refuges within and between busts. However, it is important to note that central rock-rat occupancy is currently very low (*c.* 10%) within the greater matrix of apparently suitable quartzite refuge habitat (McDonald *et al.*, 2015b). As yet there is no evidence of movement between refuges during a bust phase (P. J. McDonald, unpublished data).

*(d) Drivers of population and occupancy dynamics*

The only thoroughly documented, known-population irruption occurred in response to elevated primary productivity associated with high rainfall in 2000–2001





**Fig. 2.** Presence ( $N = 7$ ) and absence ( $N = 72$ ) records of the central rock-rat (*Zyzomys pedunculatus*) made in 1996–2002 and 2009–2014 in relation to elevation and the West MacDonnell National Park boundary, Northern Territory, Australia. An additional record was made approximately 70 km to the west, on Haast's Bluff Aboriginal Land Trust. Inset map denotes historical records (pre-1996) and the current known distribution (1996–2014) in Australia.

(Edwards, 2013a,b). At this time and over the preceding 4 years, central rock-rats occurred on a range of geology types in the Ormiston Gorge region of the West MacDonnell NP, including at sites as low as 750 m elevation. Precipitation of similar magnitude to that in 2000–2001 occurred in 2010–2011 and, although reproductive activity was observed within high-altitude refuge habitat, the species was not recorded outside of these refuges (McDonald *et al.*, 2013). Therefore, it is difficult to discuss with any certainty the factors driving population dynamics in the central rock-rat. It seems possible that the central rock-rat is suffering ongoing population declines, with its geographical range declining within successive bust phases.

#### (e) Persistence in refuges

Limited information is available on the persistence of this species in refuges during the low phase of the population cycle. The populations that irrupted during 2000–2001 and occupied habitat outside refuges went extinct during 2002 (Edwards, 2013b). A population of the central rock-rat

disappeared in 2011 from a (likely refuge) site where it had been recorded breeding 12 months prior to and during a period when individuals were breeding at another location (McDonald *et al.*, 2013). This suggests that, in contrast to arid Australia's other irruptive rodents, large rainfall events alone are not a reliable predictor of population irruptions and that, within core refuge habitat, occupancy by the central rock-rat may shift over time. Alternatively, central rock-rats may be suffering an ongoing, predation-driven decline that is resulting in reduced occupancy in refuge habitat over time and therefore a reduced ability to respond numerically to resource pulses.

### (3) Spinifex hopping-mouse, *Notomys alexis*

#### (a) Species characteristics

Distributed widely across dryland Australia, the spinifex hopping-mouse (*Notomys alexis*) is a small (body mass 27–45 g) endemic rodent (Muridae) that occurs primarily on sandy soils that can be excavated readily for burrows (Watts & Aslin, 1981). Although often present at very low density

(<0.1 animals per ha), this species can increase in numbers by more than two orders of magnitude within a year if conditions are favourable (Dickman *et al.*, 1999). As with the plains mouse and central rock-rat, females have four nipples and suckle three to four young at a time, produce multiple litters when conditions are favourable, and can extend breeding from the usual spring–summer period to autumn and winter if resources are available (Finlayson, 1940; Breed, 1979, 1992; Breed & Leigh, 2011). Population irruptions most likely arise from the extension of the usual vernal breeding period, increased survival of young, and immigration of some animals from drought-stricken areas into locales that have received recent rain (Masters, 1993; Dickman *et al.*, 1995; Breed & Leigh, 2011). The area of occupancy of the spinifex hopping-mouse expands during irruptions, with animals occupying more varied habitats at these times than during periods of rainfall deficit (Newsome & Corbett, 1975).

#### (b) *Habitat preferences*

Spinifex hopping-mice occur primarily in areas dominated by perennial hummock grasses (*Triodia* spp.), but also occur in other vegetation on alluvial flats and in shrubland dominated by chenopods, as well as in areas of low woodland and tussock grassland (Burbidge *et al.*, 1976; McKenzie, Hall & Muir, 2000; Moseby, Hill & Read, 2009). The distributional stronghold of the species is in the hummock grasslands that cover about 25% of the Australian land area (Dickman *et al.*, 2014). Unlike many other dryland-dwelling Australian rodents, there is no evidence that the geographical range of the spinifex hopping-mouse has declined; despite the dramatic fluctuations that characterise its population dynamics, it appears to be secure (Woinarski *et al.*, 2014).

#### (c) *Refuge use and type*

Despite its preference for spinifex grassland, the spinifex hopping-mouse may disappear for prolonged periods in this habitat and elude even the most determined efforts to locate it. For example, Masters (1993) captured on average  $\leq 1$  animal per plot on six 2.88-ha trapping plots in spinifex grassland over the course of a year, but within months of heavy rain the capture rate had risen to >60 animals per plot. Dickman *et al.* (1999) reported zero captures for 4 years on 12 intensively trapped 1-ha plots before animals began to reappear. Similar disappearances of this species have been recorded in most other longitudinal studies (Predavec, 1994; Southgate & Masters, 1996; Breed & Leigh, 2011). These nil-records at known sites appear to be real and do not reflect declines in detectability or trapability; Dickman *et al.* (2011) showed that independent measures of animal activity such as the presence of burrows and counts of footprints on transects correlated strongly with actual captures.

Despite the paucity of captures of spinifex hopping-mouse for prolonged periods when conditions are unfavourable, two pieces of evidence suggest that animals are still present within or close to spinifex grassland. First, remains of the species can

be recovered from the scats/pellets of mammalian and avian predators (feral cat, red fox, dingo, owls) that hunt in spinifex grassland even at times when hopping-mouse densities on sampling plots are low or zero. Although the representation of spinifex hopping-mouse in the diets of these predators may be low at these times (<10% by frequency of occurrence; Pavey *et al.*, 2008a,b; Spencer, Crowther & Dickman, 2014a), the species clearly still persists. Second, within months of a widespread rainfall event, spinifex hopping-mice reappear in traps on distantly spaced sampling plots at about the same time and in similar numbers (Dickman *et al.*, 2011). This suggests that animals are present in the spinifex grassland system all the time and are not dispersing from refuge habitats that are located in discrete or geographically remote places. Indeed, intensive surveys in other vegetation communities associated with spinifex grasslands that are often believed to provide refuge to other mammals and birds, such as riparian channels, confirm that these elements do not constitute refuge habitats for the species (Free *et al.*, 2013).

Instead, available evidence suggests that the spinifex hopping-mouse uses an unusual form of refuge habitat: tall shrubs that occur as isolates or as small stands of <10 individual plants that are embedded but widely scattered within the spinifex grassland biome (Dickman *et al.*, 2011). Radio-tracked individuals spend periods of 4–5 days within a radius of <100 m of these shrubs before moving rapidly to different shrubs that may be 2–3 km distant, presumably after the resources that the species relies upon have been reduced to marginal levels at the initial shrub sites (Murray & Dickman, 1994; Dickman *et al.*, 2011). In the eastern Simpson Desert, where the most detailed studies have been carried out, the cover of shrubs that are used by this species is no more than 6% (Greenville *et al.*, 2009). The local activity of animals around particular shrubs and rapid movement to other shrubs every few days probably accounts for the very low trappability on small, fixed sampling plots during periods when conditions are unfavourable; Dickman *et al.* (2011) suggested that most captures at these times represented individuals that were intercepted while dispersing between shrubs. If these interpretations are correct, the spinifex hopping-mouse probably makes sequential use of multiple small and highly localised refuge habitats, shifting from one refuge to the next as resources become exhausted. Thus the spinifex hopping-mouse is the species on which the shifting refuge concept used herein has been developed (Fig. 1, model 1).

#### (d) *Drivers of population and occupancy dynamics*

As for the other two case-study species, the primary driver of population increase in the spinifex hopping-mouse is rainfall. The absolute amount that is needed to be physiologically effective and to drive pulses of primary productivity varies between times and places, and the rate of population increase also is dependent on the starting level of the population and the timing of rainfall (Southgate & Masters, 1996; Dickman *et al.*, 2014). In general, winter rainfall does not appear to stimulate reproduction, whereas summers with

heavy rainfall (>200 mm) are likely to increase reproductive activity and improve the survival of young (Breed & Leigh, 2011). However, smaller amounts of summer rainfall also have stimulatory effects if winter rains have been heavy, and consecutive summers with above-average rainfall can lead to densities of >50 animals per ha (Dickman *et al.*, 2014). There is also some evidence that population increases may not occur even after very heavy summer rainfall events if an irruption has occurred within the previous 5 years or less. Ricci (2003) showed that the amount of spinifex seed produced following summer rain is a key determinant of the subsequent numbers of spinifex hopping-mice, and speculated that at least 5 years must elapse between spinifex seeding events to allow time for nutrients to recycle and become available to support further episodes of seeding.

Populations of the spinifex hopping-mouse show marked increases 3–6 months after heavy summer rains (Predavec, 1994; Dickman *et al.*, 1999), with adult animals becoming more sedentary and social as density rises (Dickman *et al.*, 2010). Sub-adults appear to be mobile during periods of population expansion, and are observed more frequently in habitats other than spinifex grassland such as claypans, shrubland and stony desert (Dickman *et al.*, 2014). In some populations social suppression of reproduction occurs when densities reach a certain threshold (>25 animals per ha; Breed, 1979, 1992), but in others the rate of population increase is slowed by declining resources and increased levels of predation from feral cats, red foxes and birds of prey (Letnic, Tamayo & Dickman, 2005; Pavey *et al.*, 2008a; Dickman *et al.*, 2010). Predation is also thought to suppress populations of spinifex hopping-mice and dampen the boom phase. Moseby *et al.* (2009) recorded 15 times more hopping-mice where predators were removed compared with sites where predators were present. High populations were sustained in the absence of predators even during dry conditions. In contrast to the plains mouse, there is no evidence of spinifex hopping-mouse declines owing to disease or increased parasite loads (Ricci, 2003).

Two further drivers are important for the spinifex hopping-mouse. In the first instance, grazing by introduced livestock can deplete food and shelter resources, reducing the average size of populations and muting their response to heavy rainfall events (Frank *et al.*, 2013). Second, fire removes vegetation cover, reduces food and shelter resources, and exposes small mammals to greater risks of predation from visually hunting predators (Letnic *et al.*, 2005; McGregor *et al.*, 2014). Small-scale fires (<10 ha) appear to have limited effects on activity or numbers, but populations decline markedly if broadscale wildfires occur (Pastro, Dickman & Letnic, 2011; Letnic, Tischler & Gordon, 2013). However, if moderate levels of vegetative cover (5–10%) are available, the spinifex hopping-mouse appears to use the sparse cover and its fast hopping speed (4.5 m/s; Stanley, 1971) to elude cursorial predators (Spencer, Crowther & Dickman, 2014b). During prolonged droughts and in the post-fire environment, tall shrubs such as mallee-form eucalypts that regenerate from

below-ground storage organs appear to provide key refuge habitat for the spinifex hopping-mouse.

#### (e) Persistence in refuges

The pattern of persistence in refuges found in the spinifex hopping-mouse contrasts markedly with that of the plains mouse and central rock-rat. This difference results from the use of shifting refuges by this species. Because the ground cover provided by the shrubs and shrub-clusters used as refuges is limited (typically 10–500 m<sup>2</sup>), hopping-mice spend less than a week at each refuge before moving to another (Dickman *et al.*, 2011). Deep leaf litter at the bases of shrubs provides both shelter and a local source of seeds and invertebrates, and it appears to be the depletion of these food resources to marginal levels that prompts animals to move on (Dickman *et al.*, 2010, 2011).

The strategy of making transient use of small and highly localised refuge habitats is likely to succeed most effectively in landscapes where the costs of moving between these patches are outweighed by the benefits of gaining access to them. Dispersal costs could be expected to be minimised if patches are in close proximity. In the eastern Simpson Desert, Tischler (2011) reported an average of 15.4 shrubs and trees (>3 m tall) per ha in spinifex grassland (range 0–20 per ha), although the proportion of these shrubs that may have been suitable for spinifex hopping-mice is not known. During the low phase of the population cycle radio-tracked hopping-mice have been recorded moving distances of 550–3340 m between patches of tall shrubs (Dickman *et al.*, 2010, 2011; C. R. Dickman, unpublished data); these distances clearly allow persistence of the species in spinifex grassland, but the effects of larger spacing between refuge habitats is not known.

#### (4) Other refuge-using species

The three case studies above cover rodents in the family Muridae all of which are endemic to the drylands of northern and central Australia where rainfall is highly unpredictable. We have used Australian murid rodents as a case study to provide focus; however, we predict that refuge use will be widespread among dryland small mammals and not only an Australian phenomenon. Rodents in the family Muridae are a diverse and widespread component of the fauna of the drylands of Asia and Africa including regions such as the Thar, Kalahari–Namib and Somali Deserts that experience highly unpredictable rainfall similar to our Australian dryland case study area (van Etten, 2009). We expect that this combination of life-history characteristics and climatic conditions will have produced conditions suitable for the evolution of refuge use in these drylands. In addition, we note that refuge use among small mammals is already known in dryland South America where several members of the family Cricetidae in the Norte Chico of north-central Chile use riverine shrublands and fog-forest patches as refuges during dry years within dominant thorn-scrub habitat (Milstead *et al.*, 2007). Small-mammal refuges also occur on the Eurasian steppe (Naumov, 1975; Bykov, Shabanova & Bukhareva, 2011).



The case studies above indicate the species-specific nature of refuges and provide a significant conceptual advance from the view of refuges as being concentrated in mesic areas such as riverine vegetation. This clarification suggests that refuges are unlikely to be shared by a large number of species. However, in some habitat types there is emerging evidence of the presence of multiple refuge-using species. As an example, the refuges of the plains mouse on cracking clay are also occupied by dasyurid marsupials including *Sminthopsis crassicaudata* and *S. macroura*. Each of these species is potentially also refuge-using. However, the current level of information is insufficient to draw conclusions on refuge-use patterns of ecologically and taxonomically similar species. The future research agenda (Section VII) provides an outline for how this knowledge can be gained rapidly.

Patterns of refuge use of most of the larger carnivorous dasyurid marsupials are currently also unclear. The brush-tailed mulgara (*Dasyercus blythi*) and crest-tailed mulgara (*D. cristicauda*) potentially use shifting refuges but available evidence is tenuous. The kowari (*Dasyuroides byrnei*) is a medium-sized (70–175 g) species that inhabits stony plains in Australia's Lake Eyre Basin where it preys on a range of invertebrates, mammals, reptiles and birds (Canty, 2012). Precipitation events and their associated plant and faunal production are the main drivers of kowari population dynamics (Lim, 1998). Available evidence suggests that it occupies fixed refuges. Sand mounds over 40 cm deep, which form in minor impermeable depressions across the landscape, are a key habitat component as they support kowari burrow systems. Sand mounds are restricted to patches in the landscape with minimal slope and small drainage depressions favourable for sand mound development. These therefore represent fixed refuges over the scale of decades.

## V. METHODOLOGY FOR REFUGE LOCATION

We develop below a three-step approach to refuge identification relying on autecological research, modelling and field verification.

Initial research should include a review of available literature on the target species and consider previous records from fauna atlases or museum databases. This information may then be used to direct field research into the target species' basic biology and ecological requirements (e.g. shelter sites, diet, reproduction, life span and movements). Optimum detection methods for the species then need to be determined and detectability should be accounted for in study design and analysis, particularly if the target species is known or likely to be imperfectly detected (MacKenzie *et al.*, 2002). Sampling should use rigorous design (e.g. stratified random) as it is ideal to establish where the target species does and does not occur in the landscape. Specifically, known absence sites can increase the predictive power of presence–absence type habitat modelling, although other techniques are available (see below). Sampling should at least be conducted during the bust period. However, sampling in

both the boom and bust periods would allow a comparison of habitat preference between these periods and could provide important insight into the ecological drivers of the refuges. Location information obtained from previous bust periods and/or field sampling can then be used broadly to identify potential refuge habitat of the species. Landscape-scale identification of potential refuge sites could be based on a number of physical or temporal habitat attributes including soil or rock type, elevation, patch size, fire age, rainfall and vegetation. Locating potential refuges therefore may be as simple as identifying a single landform type on a map or could use one of a range of species distribution modelling tools. For example, generalised linear models are frequently applied to presence–absence data to build habitat models and are readily incorporated into global imaging system (GIS) programs to produce probability of occurrence maps (Elith & Leathwick, 2009). More complex non-linear models (e.g. generalised additive models, multivariate adaptive regression splines) can also be used to predict distributions and may outperform the more established methods (Elith *et al.*, 2006). Powerful machine-learning programs are also available (e.g. Maxent) and can be used to model distributions with presence-only data (Phillips & Dudik, 2008).

Regardless of the modelling technique used to identify potential refuge sites at a landscape scale, field verification is required to confirm presence during a bust period and determine whether hypothesised refuge areas actually facilitate persistence of the target species during the bust. Ideally, a range of predicted absence sites should also be sampled at this time to ensure rigorous validation of the habitat models. The results can then be used to refine habitat models if required (Luck, 2002). This sampling is also important so that refuge characteristics operating at finer scales than the available map layers can be identified, and a range of outbreak and potential refuge sites should be monitored and compared during the bust phase. To verify correctly a species' refuge, the species' presence and persistence should ideally be recorded during two successive bust periods. While a larger number of sampling periods would be ideal, the rarity of boom periods means that verification during more than two bust periods could take decades. Two bust periods is a reasonable balance between minimising the possibility of presence due to migration or chance, and the ongoing scarcity of long-term monitoring programmes in dryland areas.

This stage should include field-based techniques designed to identify species presence at a site level as well as methods designed to test for evidence of within-bust persistence (reproduction, immigration or longevity). While difficult to anticipate, field surveys to record presence/absence in potential refuge sites should ideally occur towards the end of the bust cycle. Evidence of persistence may require capture–mark–recapture studies and recording of reproductive condition and age if the species' life span is shorter than the average bust period. It is important at this stage to identify fine-scale habitat attributes that characterise refuges so that field monitoring will be able to include



measurements of specific habitat variables at both hypothesised refuge and outbreak sites. Once these steps have been completed, species distribution models can be updated and used to identify potential species-specific refuge sites at a landscape scale. If required, the presence of fine-scale site characteristics can then be used to verify or prioritise specific refuges during confirmatory ground-truthing exercises.

## VI. POTENTIAL THREATS

In the drylands of Australia, factors considered to have contributed to declines of refuge-using small mammals include altered fire regimes (e.g. Cockburn, 1978), environmental degradation from grazing by livestock and feral herbivores (Smith & Quin, 1996; Lunney, 2001), predation from introduced carnivores (Dickman *et al.*, 1993; Johnson, 2006), and epidemic disease (Abbott, 2006; Green, 2014). The relative importance of these threats has been difficult to quantify, with a multitude of causal factors probably contributing. However, modelling (e.g. Smith & Quin, 1996; McKenzie *et al.*, 2007), dietary analysis (e.g. Corbett & Newsome, 1987; Kutt, 2012) and field-based experimental evidence (e.g. Kinnear, Onus & Bromilow, 1988; Predavec & Dickman, 1994; Moseby *et al.*, 2009) increasingly implicates predation as the highest order cause of present-day declines of small mammals. Aridity, low reproductive rates and small body size are, in turn, believed to increase vulnerability to predation (Smith & Quin, 1996; McKenzie *et al.*, 2007).

The presence and use of biophysical structures that shelter small mammals, such as optimal-aged spinifex patches or soil textures that allow for digging or the production of cracks, has minimised range reductions in a number of small mammal species (Smith & Quin, 1996; Burbidge & Manly, 2002). While there is sometimes little relationship between vegetation structure and small mammal populations (Letnic & Dickman, 2010), this may not be the case during periods of high predator activity (Letnic *et al.*, 2005) particularly at sites of high small mammal density such as refuges. For species such as the plains mouse, cracking clays provide both resources and shelter against predation by birds and mammals (Brandle *et al.*, 1999). Altered surface hydrology may cause flooding or the deposition of silt and sand from upslope areas, leading to a temporary or more permanent loss of shelter and food resources, and downgrading of these areas to secondary habitat (Brandle *et al.*, 1999).

Although poorly examined in the Australian drylands, changes in surface hydrology, soil microtopography and surface integrity can potentially change the availability of food in refuges. Most small mammals in the Australian drylands do not require free-standing water to survive (Watts & Aslin, 1981). Although these species can subsist during bust periods on invertebrates, dry seed, and whatever green material is available (Murray *et al.*, 1999), during boom periods primary productivity needs to be sufficient to produce the seeds that are an important part of the bust-period diets of small mammals (Watts & Aslin, 1981). Changes in surface hydrology

can reduce soil moisture, and therefore primary productivity, with high levels of herbivory reducing seed production in the short term and primary productivity in the longer term (Whitford, 1995; Ludwig *et al.*, 2005). That said, the scant empirical data that are available suggest that fire and grazing may have little effect on some refuge-using species during boom periods (D'Souza *et al.*, 2013; Frank *et al.*, 2014), and the opportunistic and omnivorous diets of many dryland-dwelling rodents (Murray *et al.*, 1999) may potentially buffer the dietary restrictions associated with declining biomass.

Changing species interactions pose a threat to small mammal refuges when these involve an increase in absolute levels of predation or competition, or if the amplitude of population cycles alters such that relative levels of predation or competition increase during significant periods. Increased densities of mesopredators such as foxes or cats through, for example, an increase in artificial waterpoints (Brawata & Neeman, 2011) or a decline in dingo numbers (see Letnic, Ritchie & Dickman, 2012), are an obvious and direct threat to small mammal species reliant on refuges. This risk can be multiplied if refuge habitats are subjected to structural changes (Letnic & Dickman, 2010). Refuge-using species may be particularly vulnerable to predation by mesopredators during the shift between boom and bust periods. During this time, population densities of refuge species may become relatively more concentrated in refuge areas than in the surrounding landscape and, with densities of alternative prey sources beginning to decline, predators may target refuges (Newsome & Corbett, 1975; Smith & Quin, 1996; Letnic & Dickman, 2010; Pavey *et al.*, 2014a). Although a few dispersed individuals could be the founders of new colonies after predator starvation, this mechanism may explain why plains mouse refuges can disappear despite the availability of abundant food (Watts & Aslin, 1981). Species using shifting refuges may therefore be less vulnerable to localised change than those that are spatially fixed, as widespread and frequent movement allows for minimisation of predation risk at any one refuge (Newsome & Corbett, 1975).

Climate change may affect refuges and refuge-using species *via* direct physiological or habitat impacts, or by altering the amplitude of population cycles. Temperatures are generally expected to increase in dryland Australia but there is significant uncertainty associated with expected changes in precipitation (Healy, 2015). Given that precipitation is the primary determinant of the dynamics of small mammals with life histories that allow opportunistic breeding, this uncertainty is unfortunate. That said, modelling of the regional climate of the Simpson Desert does suggest an accelerating trend for larger and more frequent rainfall events that punctuate periods of extreme drought (Greenville, Wardle & Dickman, 2012) and recent research suggests a doubling of extreme La Niña events globally (Cai *et al.*, 2015). Changes in these stochastic events are expected to exaggerate the amplitude of population cycles and increase the risks associated with extreme population fluctuations.

The ability of refuges to buffer temperature changes in future will be a product of a variety of factors including soil

type and burrow or crack depth, as is the case currently (Geiser & Pavey, 2007; Körtner, Pavey & Geiser, 2008). While fire and predation are current postulated threats to the central rock-rat (McDonald *et al.*, 2013), climate-change modelling suggests there will be no suitable habitat available for this species by 2085 (A. Reside, unpublished data, see Reside *et al.*, 2013). The Barkly Tableland and Lake Eyre Basin may contain the majority of refuges for the long-haired rat (Plomley, 1972; Carstairs, 1974; Newsome & Corbett, 1975) but again modelling suggests there will be no suitable habitat in this region for the species by 2085 (A. Reside, unpublished data, see Reside *et al.*, 2013).

Current ecological knowledge suggests that the changing amplitude of population cycles, either through ongoing ecological perturbations in post-colonial landscapes like Australia or through climate change, may pose a more subtle threat to refuges than implied by suitable climate-change envelopes. Most research to date shows refuge species to be in good body condition and reproductive status during bust periods (Brandle *et al.*, 1999; Pavey *et al.*, 2014a), and that this may be due to low levels of resources that become periodically available during localised, bust-period precipitation events (Newsome & Corbett, 1975; Nano & Pavey, 2013; Pavey & Nano, 2013). Dickman *et al.* (1999) rejected the hypothesis that too-frequent heavy rain could potentially have a negative effect on food stores on the basis that Australian dryland rodents do not cache food. However, changes in the temporal and spatial variability or intensity of precipitation events may change food resources, fecundity, and population viability in other ways during bust periods. The dampening of booms may affect outbreeding and increase predation risk; the probability of a population irruption of the long-haired rat increases rapidly after annual rainfall of 600 mm, with an 80% probability of an irruption occurring after annual rainfall of 750 mm (Greenville *et al.*, 2013), but changes in the period between such events may affect population viability.

The changing amplitude of boom–bust cycles may also affect predator–prey relationships by affecting the length or severity of Smith & Quin's (1996) 'predator pit'. Currently, the high mortality rate of mesopredators during the bust phase (Newsome & Corbett, 1975) allows refuge species to reproduce when localised resources become available and predation risk is low. It is likely that predators suppress small mammals only when boom periods are close enough for them to survive, despite a major bust-period reduction in their food supply (Newsome & Corbett, 1975). Predator die-off may not occur if climatic patterns shorten periods between booms. Boom–bust amplitudes and frequency thus affected may provide alternative food sources to mesopredators (which are generalist feeders, e.g. Kutt, 2012; Mifsud & Woolley, 2012), dampening their high mortality rate. Refuge-using prey species may not be similarly advantaged (see Dickman *et al.*, 1999) but their exposure to these mesopredators will be extended and potentially ongoing, increasing their risk of extinction within their refuges. The small size and limited connectivity of refuges are endogenous features that may increase the vulnerability

of their inhabitants. Brandle *et al.* (1999) found genetic subpopulations, but little evidence of inbreeding, in wild populations of plains mice. Lacy & Horner (1997) noted that boom–bust cycles may provide optimal conditions for the purging of deleterious alleles expressed through inbreeding in the long-haired rat. Nevertheless, irruptions interspersed with contractions to refuges could theoretically still lead to inbreeding during bust periods (Lacy & Horner, 1997). Recent developments in landscape genetics could be used to quantify such possibilities (Galpern *et al.*, 2014).

## VII. FUTURE RESEARCH AGENDA

An ongoing research agenda should focus on four key questions. First, what constitutes a refuge, particularly one that is of high quality? Second, what are the spatial and temporal population interactions within and among refuges, and how might these interactions relate to long-term species survivorship? Third, what is the nature of threats to refuge quality and connectivity? Finally, how widely applicable is the refuge concept, both geographically and taxonomically, beyond irruptive mammals?

The refuge typology proposed herein highlights the diversity of potential refuge forms, but it is the case studies that suggest that what constitutes a refuge, and high refuge quality, is likely to be species-specific. This specificity involves interactions between species behavioural traits, dietary and microclimate requirements, and reproductive characteristics. It is thus likely that there is no easy answer to the question of what constitutes a refuge. Similarly, it is likely that there will be no one location where managers can target effort in an attempt to improve refuge quality for a large number of species. However, it remains possible that multiple species may occupy similar refuge habitat, as is suggested above (Section IV.4) for the plains mouse and several species of small dasyurid marsupials. This possibility requires further investigation as it will enable more efficient management to be undertaken.

Understanding population interactions within and among refuges, and how these might relate to long-term species survivorship, is an important part of clarifying the temporal and spatial boundaries of refuges better, and understanding patterns of gene flow and population viability. A fundamental aspect of this work will be to understand the fate of individuals in expanded populations (i.e. those that move outside refuges during booms) during contraction phases when busts begin. The key question is whether populations outside refuges make any contribution to the long-term evolution of the species (Stewart *et al.*, 2010). This understanding is important for the design of management strategies. For example, currently it is unclear whether management should be focussed at the very small scale of a refuge (sometimes only a few hectares), or whether broader connectivity issues at the landscape scale make the management of inter-refuge corridors equally important. Clarifying the scale of connectivity through time and space will be an important step.

Some of the hypothesised threats highlighted above, including high levels of predation at key times in the population cycle and potential shifts in population amplitudes with climate change, are threats likely to be applicable to all refuge-using mammals. Our knowledge on the extent and severity of these threats will need to be refined with an increase in more temporally nuanced understanding of climatic drivers and species responses. Longitudinal assessments of species interactions and landscape ecology that are embedded within their climatic context will be a key requirement.

Finally, this review has necessarily focused on the small mammal refuges in dryland Australia as this is the dryland system where this concept and its field assessment have been pioneered and developed. The applicability of the refuge typology outlined herein to those outside Australia, and the suitability of the suggested methods for identifying refuges and potential threats are as yet unclear. It is similarly unclear as to whether the overall patterns and processes of refuges can be applied outside of the small mammal context. Could the boom period colonisation and bust period retreat of some dryland plants be functionally analogous to the use of a refuge, for example? We therefore encourage the refinement of the refuge concept in light of global research across a range of taxa.

## VIII. CONCLUSIONS

(1) Refuges of dryland fauna are little known and available information is disparate. In this review we have synthesised available information and provided conceptual advances in recognition and delineation of refuge types; application of refuge ideas to boom–bust environments and the recognition that not all refuges are fixed within the landscape; the variable nature of refuges and the resulting biological consequences; and the approaches needed to locate and manage refuges.

(2) A wide range of dryland-dwelling fauna with irruptive population dynamics contract to refuges during the bust phase of their population cycles. For dryland small mammals, these refuges differ from the refugia occupied by fauna and flora in response to changing climate in being occupied for shorter timescales (months to years as opposed to millennia) and being smaller in size.

(3) Irruptive small mammals may occupy refuges that are relatively fixed in location or (more rarely) refuges as small as groups of trees or shrubs that shift in suitability regularly at short timescales of days or weeks. Available evidence suggests that refuge type and usage patterns are species-specific. It is possible that multiple species may share the same refuge habitat if the ecology and environmental requirements of the species overlap, but available evidence suggests that this is rare. Three case studies of dryland rodent species show variation across species in refuge location, occupancy patterns and stability.

(4) Refuges are vital locations for the conservation management of irruptive dryland mammals. It appears likely that local populations of such irruptive species located outside of refuges go extinct as the landscape dries following each boom period. Therefore, refuges are the only locations occupied by irruptive species for the duration of the long bust periods. The small size of refuges makes them highly vulnerable to threatening processes. Known and potential threats to refuges include predation by introduced carnivores, structural changes to the environment leading to a reduction in availability of shelter and food, climate change and stochastic factors resulting from the small size and limited connectivity of the refuges.

(5) The small size and associated high vulnerability of refuges, their species-specific nature, and their use by globally threatened fauna such as the plains mouse and central rock-rat make the identification of locations and management of refuges of dryland fauna a high priority. However, the information we summarise here indicates that refuges comprise a small portion of the landscapes they occupy and will not be detected during standardised faunal surveys or, most likely, by remote-sensing methods. Therefore, refuges need to be searched for using specific approaches. Our three-step approach will maximise the success of such targeted searches.

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