

Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats

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ABSTRACT

Resources are produced in pulses in many terrestrial environments, and have important effects on the population dynamics and assemblage structure of animals that consume them. Resource-pulsing is particularly dramatic in Australian desert environments owing to marked spatial and temporal variability in rainfall, and thus primary productivity. Here, we first review how Australia's desert mammals respond to fluctuations in resource production, and evaluate the merits of three currently accepted models (the ecological refuge, predator refuge and fire-mosaic models) as explanations of the observed dynamics. We then integrate elements of these models into a novel state-and-transition model and apply it to well-studied small mammal assemblages that inhabit the vast hummock grassland, or spinifex, landscapes of the continental inland. The model has four states that are defined by differences in species composition and abundance, and eight transitions or processes that prompt shifts from one state to another. Using this model as a template, we construct three further models to explain mammalian dynamics in cracking soil habitats of the Lake Eyre Basin, gibber plains of the Channel Country, and the chenopod shrublands of arid southern Australia. As non-equilibrium concepts that recognise the strongly intermittent nature of resource pulsing in arid Australia, state-and-transition models provide useful descriptors of both spatial and temporal patterns in mammal assemblages. The models should help managers to identify when and where to implement interventions to conserve native mammals, such as control burns, reduced grazing or predator management. The models also should improve understanding of the potential effects of future climate change on mammal assemblages in arid environments in general. We conclude by proposing several tests that could be used to refine the models and guide further research.

Key words: bottom-up *versus* top-down, climatic oscillations, alternative stable states, predation, small mammal, trophic cascade, resource pulse, refuge, fire.

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I. INTRODUCTION

Resources are produced intermittently in many terrestrial environments, and have important effects on the population dynamics of organisms that exploit them. In seasonal environments, for example, consumers usually breed when resources increase and achieve peak densities during periods of resource abundance (Caughley & Sinclair, 1994). In spatially heterogeneous environments, by contrast, mobile consumers frequently track resources and redistribute themselves among patches that provide surety of resource access (Law & Dickman, 1998). If resource production is highly sporadic, consumers may adopt a range of ‘holding’ strategies during periods of shortage, and then erupt in large numbers when conditions are favourable (Whitford, 2002). Environments with strongly pulsed resources provide opportunities to quantify the effects of ‘bottom-up’ influences on population dynamics, and to assess how ‘top-down’ processes such as predation and competition vary in strength and importance over time (Ostfeld & Keesing, 2000; Bruno, Stachowicz & Bertness, 2003). These environments also provide unique understanding of the genetic and eco-physiological responses of consumers to resource uncertainty (Bradshaw, 2003; Vega *et al.*, 2007), and allow insight into how organisms will respond to more frequent and increasingly extreme weather events as the global climate changes (Grosbois *et al.*, 2008).

Strong resource pulsing can occur in environments that sustain periodic outbreaks of palatable insects such as cicadas or locusts (Yang, 2004; Ostfeld & Keesing, 2007), environments that receive large but intermittent resource subsidies from floods or storms (e.g. beached algae or marine animals; Catenazzi & Donnelly, 2007; Lewis *et al.*, 2007), and other environments where localised wind events dump fruit, wood and other forest canopy resources on the ground for terrestrial consumers (Bouget & Duelli, 2004). Large but intermittent pulses of flowers and seeds (mast events) also are produced by trees and other perennial plant species at mid-latitudes (Koenig & Knops, 2000; Kelly & Sork, 2002), triggering dramatic population increases in granivorous insects, birds and mammals (Ostfeld, Jones & Wolff, 1996; Murúa, Gonzalez & Lima, 2003; Li & Zhang, 2007).

Although intermittent resource production occurs in many environments, it is perhaps most extreme in arid systems that are characterised by high temporal and spatial variability in rainfall. Temporal variability in precipitation

generally increases with decreasing annual rainfall (Low, 1979), so that differences in rainfall in very arid regions may exceed an order of magnitude between years (Robinson, 1990). More importantly, in hot deserts where potential evapo-transpiration is high, plants may respond only to rainfall inputs above a particular threshold (Du Plessis, 1999); it is these physiologically-effective rains that are particularly variable in both time and space in arid regions (Whitford, 2002).

Several authors have proposed that strongly intermittent pulses of productivity in arid environments can be exploited most easily by consumers with desiccation-resistant resting stages, such as many invertebrates, or low energy requirements, such as ectothermic vertebrates (e.g. Pianka, 1986; Cloudsley-Thompson, 1991; Dickman, Lunney & Burgin, 2007). However, mammals are conspicuously successful inhabitants of many arid regions, and recent research has uncovered a range of behavioural, physiological and ecological adaptations that allow them to persist (Degen, 1997; Geiser, 2004; Idris, 2005). On the one hand, research has been stimulated by concerns about eruptions of granivorous or herbivorous mammals in areas used for cereal cropping (White, 2002) or by fears about zoonotic disease outbreaks (Hjelle & Glass, 2000; Jaksic & Lima, 2003; Ahuja, 2005). On the other hand, some investigations have focused on the vulnerability of native desert mammals when productivity cycles are disrupted by broadscale agricultural practices and introduced predator species (Dickman, 1996a; Sinclair *et al.*, 1998; Shapira, Sultan & Shanas, 2008). A common quest in much of this research has been to understand how populations and assemblages of mammals respond to pulses in productivity so that systems can be better managed for both conservation and production goals (Blackwell *et al.*, 2003).

In the present paper, we begin by reviewing the dynamics of mammals in arid Australia. Productivity in much of the continental inland is highly variable in time and space, and populations of some mammal species have long been known to fluctuate wildly in response (Bennett, 1887; Plomley, 1972). The ephemeral nature of many mammal populations poses considerable problems for wildlife managers charged with protecting agricultural interests and, especially, conserving biodiversity. The key problems lie in predicting when and where eruptions will occur, whether eruptions will drive numerical increases in populations of introduced predators and, importantly, the potential effects that such increases may have on populations of rare and vulnerable species (Sinclair

et al., 1998; Letnic, Tamayo & Dickman, 2005). Australia's arid regions already have suffered losses of some 23 species of native mammals over the last 200 years (McKenzie *et al.*, 2007), and there is little indication that this extinction cascade has stopped (Letnic & Dickman, 2006). The problems for managers are further complicated by observations that many mammals in arid Australia do not show predictable patterns of habitat use (Dickman & Read, 1992; Murray & Dickman, 1994; Paltridge & Southgate, 2001; Masters, Dickman & Crowther, 2003; Letnic, 2003; Letnic *et al.*, 2004; Körtner, Pavey & Geiser, 2007). As a consequence, habitat modifications that use tools such as fire and grazing pressure may not provide predictable management outcomes.

We next present a conceptual model that attempts to explain the dynamics of small mammal populations in the vast spinifex (hummock) grasslands of arid Australia. Spinifex grasslands, dominated by species of *Triodia*, are the major biome of the inland deserts (Fig. 1) and cover some 2 010 000 km², or approximately 22%, of the continent (Griffin, 1984). The model is intended to provide a conceptual framework for describing and managing small mammal populations and, by extrapolation, other fauna that interact with small mammals. Because the dynamics of small mammal assemblages in other biomes of arid Australia are similar in many respects to those of small mammals in the spinifex grasslands, we also present generalised conceptual models for other habitat types where suitable data exist. Because our model is structured around the occurrence of intermittent resource pulses we believe that the broad principles and approach outlined in the model may provide a useful framework for the management of small mammal populations in other environments where resource pulses are major demographic drivers.

We begin by outlining the physical environment of arid Australia, placing particular emphasis on rainfall and its effects on primary productivity. We then review three existing models that explain the organisation of mammal assemblages, and introduce our model by outlining a series of observations about small mammal populations that we believe are important to understanding their dynamics. These observations are then incorporated into the conceptual model. We conclude by discussing potential studies that could be used in future to test, develop and refine the model that we present.

II. CLIMATE AND LANDSCAPE IN ARID AUSTRALIA

The arid and semi-arid zones occupy about 70% of Australia's land surface, encompass numerous land forms and vegetation types, and are characterised by low and sporadic rainfall with high potential evapo-transpiration. The arid zone is bound in the north by the 750 mm rainfall isohyet, the 250 mm isohyet in the south and along the west coast, and the 500 mm isohyet to the east (Young, 1979). The northern regions are hot year round with more rain

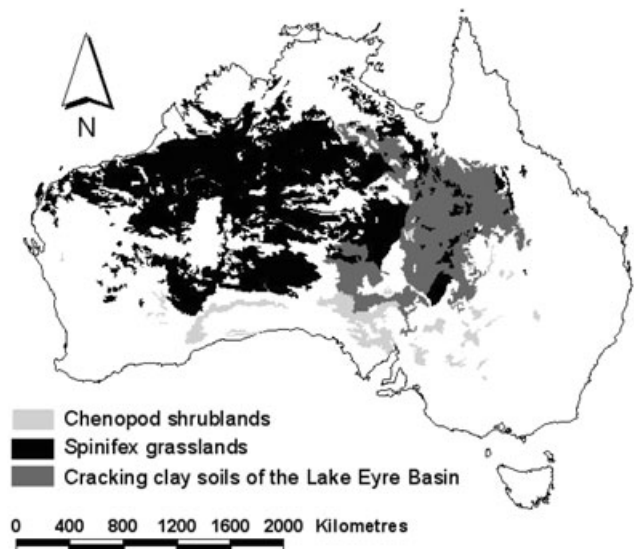


Fig. 1. The distribution in Australia of spinifex (*Triodia* spp.) grasslands, chenopod shrublands and the cracking clay soils of the Lake Eyre Basin.

falling during late summer and autumn than at other times. The southern regions are characterised by hot summers and cold winters with rainfall tending to occur mainly during winter. Many of the landforms of arid Australia are ancient and consequently have been subject to extensive weathering. For these reasons the arid zone is relatively flat and possesses extremely poor, nutrient-deficient soils (Stafford Smith & Morton, 1990; Orians & Milewski, 2007). The most distinctive and important vegetation types in the Australian arid zone are hummock grasslands, eucalypt woodlands, *Acacia* woodlands, Mitchell grasslands, chenopod shrublands and stony deserts (Harrington, Wilson & Young, 1984). As the most extensive of the inland biomes, hummock grasslands occur in both the summer- and winter-dominated rainfall regions.

Due to the importance of rainfall in determining biological activity at all trophic levels, desert ecosystems have frequently been described as being 'water-controlled' (Noy-Meir, 1973; Ludwig *et al.*, 1997; Holmgren *et al.*, 2006a, b). Whereas seasonal rainfall regimes in many of the world's deserts exhibit moderate predictability (Evenari, Noy-Meir & Goodall, 1985), the occurrence and intensity of rainfall in the Australian arid zone is highly variable both in time and space (Stafford Smith & Morton, 1990; Nicholls, 1991). In northern and eastern Australia, the occurrence of rainfall is influenced strongly by the El Niño/Southern Oscillation (ENSO) (Nicholls, 1991; Chiew *et al.*, 1998) which, in turn, reflects circulations of currents in the Pacific Ocean (Diaz & Markgraf, 1992). The two extremes of the ENSO phenomenon are known as La Niña and El Niño and, in Australia, are associated with above-average and below-average rainfalls, respectively (Nicholls, 1991). The strong influence of the ENSO on the Australian climate results in large inter-annual variability in rainfall, with droughts and

wet periods having time scales of about a year. When they occur, both El Niño and La Niña events normally start early in the calendar year and cease early in the following year (Nicholls, 1991). Thus the ENSO has been described as being 'phase-locked' to the calendar year (Nicholls, 1991). Another characteristic of the influence of the ENSO on the Australian climate is that El Niño and La Niña events may follow each other, resulting in extreme year to year changes in rainfall (Nicholls, 1991).

III. THE RELATIONSHIP BETWEEN RAINFALL, PRIMARY PRODUCTIVITY AND WILDLIFE POPULATIONS IN ARID AUSTRALIA

Scarcity of water generally limits primary productivity in arid environments. Rainfalls trigger biological, physical and chemical activities that result in pulses of increased primary productivity (Noy-Meir, 1973; Ludwig *et al.*, 1997; White, 2008). The magnitude and duration of these rain-driven pulses depends on the size of the rainfall event, soil structure and the availability of nutrients and seeds in the soil seed bank (Ludwig *et al.*, 1997; Huxman *et al.*, 2004). In arid Australia, small to moderate rainfalls stimulate growth pulses by perennial plants and the germination of short-lived plant species (Westoby, 1979; Hunter & Melville, 1994; Ludwig *et al.*, 1997). Exceptionally large rainfalls, by contrast, can prompt major biotic changes that include widespread germination and growth of ephemeral, annual and perennial plant species and the recruitment of perennials such as trees and shrubs (Stafford Smith & Morton, 1990; James, Landsberg & Morton, 1995; Ludwig *et al.*, 1997; Orians & Milewski, 2007).

As in other arid regions of the world (Brown & Zeng, 1989; Meserve *et al.*, 1995; Jaksic *et al.*, 1997; Whitford, 2002), the population dynamics of many vertebrate species in arid Australia are influenced strongly by rainfall-driven bursts of primary productivity (McCarthy, 1996; Short *et al.*, 1997; Dickman *et al.*, 1999b; Dickman, Letnic & Mahon, 1999a; Kingsford, Curtin & Porter 1999a; Kingsford *et al.*, 1999b; Chan, 2001). There is also an increasing body of evidence to suggest that predation and its interaction with climatic conditions may be important in regulating the populations of some mammal species in arid regions of both Australia and South America (Newsome & Corbett, 1975; Newsome, Parer & Catling, 1989; Meserve *et al.*, 1996, 2003; Jaksic *et al.*, 1997; Pavey, Eldridge & Heywood, 2008; Letnic, Crowther & Koch, 2009a; Letnic *et al.*, 2009b). Furthermore, in Australia, there is evidence that the impacts of predation on wildlife may interact with land-management practices associated with livestock grazing (Caughley *et al.*, 1980; Pople *et al.*, 2000; Newsome *et al.*, 2001; Salo *et al.*, 2007; Letnic *et al.*, 2009a, b; Letnic & Koch, 2010). In particular, removal of vegetation by fire, grazing, clearing or other practices reduces the structural complexity of habitats, and thus allows predators greater access to prey (Dickman, 1996a, b; Letnic *et al.*, 2005).

Populations of rodents, peramelids, potoroids and macropodids generally increase in response to periods of high rainfall and decline during periods of rainfall deficiency (Robinson *et al.*, 1994; McCarthy, 1996; Short & Turner, 1999; Dickman *et al.*, 1999b; Pople *et al.*, 2000; Sharp & Norton, 2000). Dramatic outbreaks of native and introduced rodents have been observed following exceptional rainfalls (Crombie, 1944; Plomley, 1972; Newsome & Corbett, 1975; Saunders & Giles, 1977; Predavec, 1994a, b; Predavec & Dickman, 1994; Brandle & Moseby, 1999; Dickman *et al.*, 1999b; Letnic *et al.*, 2005; Pavey *et al.*, 2008). Insectivorous dasyurid marsupials, on the other hand, do not always exhibit such marked responses to rainfall and may even decline following large rainfall events (Morton & Martin, 1979; Woolley, 1984; Bos & Carthew, 2001; Dickman *et al.*, 2001; Gilfillan, 2001; Haythornthwaite & Dickman, 2006a). The carnivorous dasyurids *Dasyurus blythi* and *D. cristicauda* undergo dramatic increases in abundance following large rainfall events, possibly due to their exploitation of erupting rodent populations (Chen, Dickman & Thompson, 1998; Masters, 1998; Letnic *et al.*, 2005). Populations of introduced herbivores: rabbits (*Oryctolagus cuniculus*), goats (*Capra hircus*), horses (*Equus caballus*), donkeys (*Equus asinus*), hares (*Lepus capensis*) and feral pigs (*Sus scrofa*), also undergo fluctuations in response to rainfall (Myers & Parker, 1975a, b; Parer, 1977; Woodall, 1983; Newsome *et al.*, 1989; Wilson *et al.*, 1992; Choquenot, McIlroy & Korn, 1996; Pople *et al.*, 1996; Risbey *et al.*, 2000), but show different time lags that probably relate to differences in their intrinsic rates of increase.

The population dynamics and diets of avian and larger mammalian predators such as the dingo (*Canis lupus dingo*), red fox (*Vulpes vulpes*) and cat (*Felis catus*), appear to be influenced strongly by the abundance of smaller mammals and thus, indirectly, by rainfall-driven pulses of productivity (Plomley, 1972; Morton *et al.*, 1977; Morton & Martin, 1979; Corbett & Newsome, 1987; Newsome *et al.*, 1989; Thomson, 1992; Pople *et al.*, 2000; Aumann, 2001; Read & Bowen, 2001; Paltridge, 2002; Pavey *et al.*, 2008). These increases probably reflect both successful recruitment and migration (Aumann, 2001). During periods of low rainfall, when populations of small mammals decrease, predators undergo reductions in abundance (Newsome & Corbett, 1975; Pople *et al.*, 2000; Aumann, 2001) and often switch their diets to other taxa, particularly reptiles (Paltridge, 2002).

IV. CURRENT MODELS EXPLAINING MAMMALIAN POPULATION DYNAMICS AND ASSEMBLAGE COMPOSITION IN ARID AUSTRALIA

(1) Ecological refuge model

The ecological refuge model is perhaps the most developed and widely cited model to explain the dynamics of mammal populations in arid Australia. This model is best described as a habitat-focused model, and was developed from

the concept of ecological refugia (Newsome & Corbett, 1975; Carstairs, 1976). Ecological refugia are generally considered to be places where animal species can persist through drought owing to the existence of relatively dependable supplies of moisture and nutrients (Morton & Baynes, 1985; Morton, 1990). Movements of animals among refuges probably increase the persistence of regional metapopulations (Harrison, 1991), and refuges themselves may act as source areas for emigrants to the surrounding landscape when favourable climatic conditions prevail (Watts & Aslin, 1974; Carstairs, 1976; Brandle & Moseby, 1999). Refuges are often associated with geographical features such as rocky ranges and low-lying drainage basins where the availability of nutrients and moisture is greater than in the surrounding landscape (Brandle & Moseby, 1999; Read, Copley & Bird, 1999). Areas that have received localised rains have also been postulated to serve as ephemeral refuge habitats (Newsome & Corbett, 1975). Consequently, refuges have been conceptualised as being either fixed patches in the landscape or entities that shift geographically in response to rainfall patterns (Newsome & Corbett, 1975, see also Morton, Short & Barker, 1995).

The ecological refuge model has been linked to observations of nomadism and migration by small mammals (Dickman, Predavec & Downey, 1995; Letnic, 2002). It has been proposed, in particular, that the very high mobility of many small mammal species in arid Australian habitats (distances >5 km have been commonly recorded) is an adaptive response that allows individuals to locate temporary but food-rich refuges during times of rainfall deficiency rather than relying upon cached food (Newsome & Corbett, 1975; Dickman *et al.*, 1995; Haythornthwaite & Dickman, 2006b) and waiting for future rains. Similar itinerant movements towards areas that have recently received rain and exhibit temporarily high primary productivity have been documented among kangaroos and several species of inland birds (Newsome, 1965, 1971; Denny, 1982; Davies, 1984). The concept of 'rainfall refuges' is supported by observations that mammals are often more abundant in areas that have received heavy rainfall at local (<100 km²) and regional scales (>500 km²) (Paltridge & Southgate, 2001; Letnic & Dickman, 2005). Long-distance movements (>5 km) appear to be very rare events among small and even medium-sized mammals in other world deserts (Degen, 1997), and perhaps emphasise the spatially and temporally unpredictable distributions of resources that characterise arid Australian habitats.

Despite the intuitive appeal of the ecological refuge model and observations that mammals often focus upon productive patches when they appear in the landscape, empirical support for this model is mixed. On the one hand, studies conducted in sandplain and sandridge deserts have found little correlation between the abundance of small and medium-sized mammal species and geographic features such as drainage basins or riparian strips (Paltridge & Southgate, 2001; Haythornthwaite & Dickman, 2006a; Southgate *et al.*, 2007). In these studies small mammals

were either equally common among habitats of differing productivity, or responsive to the locally prevailing climatic conditions. On the other hand, studies carried out in cracking clay soil habitats have shown that both dasyurid marsupials and native rodents can persist through droughts by using low-lying areas with deep soil cracks and accumulations of prey and organic matter within them for food and shelter (Carstairs, 1976; Andrew & Settle, 1982; Read, 1984c; Brandle & Moseby, 1999). Rocky ranges commonly also support larger populations or more species of mammals (How & Cooper, 2002), presumably because they offer a range of attributes that insure against poor conditions. These attributes include shelter from predation, shelter from fire, greater habitat diversity, more dependable food resources and less demands on moisture and thermoregulation than in surrounding plains habitats (Burbidge & McKenzie, 1989; Dickman *et al.*, 1993b; Gilfillan, 2001; Pavey, Goodship & Geiser, 2003). The greater species richness of rocky range habitats may also be explained by the presence of specialist saxicolous species that are restricted to these habitats (Dunlop & Sawle, 1980; How & Cooper, 2002).

Given high spatial variability in rainfall and stochastic factors influencing population survival, it is likely that small mammal populations often persist through drought as metapopulations in refuge habitats rather than in specific refuge patches (Brandle & Moseby, 1999). Thus it is unlikely that any specific habitat patch will serve as a refuge during all droughts. Widespread rainfalls and subsequent population increases, particularly those associated with the La Niña phase of the ENSO (Nicholls, 1991; Letnic *et al.*, 2005), appear to provide the opportunity for refuge populations to disperse, thus allowing the exchange of genetic material between populations and, when populations inevitably decline (owing to drought and predation), the establishment of new metapopulations. Some of these metapopulations are likely to persist in turn as refuge populations through future droughts, and so continue the cycle of boom and bust.

(2) Predator refuge model

Studies reporting inverse relationships between predator abundance and the abundance of small and medium-sized mammals indicate that predation, particularly by introduced species such as foxes and cats, can have major effects on population and assemblage dynamics in arid Australia (Corbett & Newsome, 1987; Newsome *et al.*, 1989; Read, 1997; Risbey *et al.*, 2000; Kinnear, Sumner & Onus, 2002; Letnic *et al.*, 2009a, b; Moseby, Hill & Read, 2009). Reports of inverse relationships between the abundances of small mammals and introduced predators have been obtained in studies comparing predator-free island habitats with mainland habitats (Read, 1997), experimental units with differing levels of predators (Risbey *et al.*, 2000; Letnic *et al.*, 2009a, b; Moseby *et al.*, 2009), and in longitudinal tracking of population dynamics (Corbett & Newsome, 1987; Letnic *et al.*, 2005; Pavey *et al.*, 2008).

Collectively these studies indicate that the abundance of predators and, in turn small mammals, can be influenced

by environmental factors that result from climatic events (Corbett & Newsome, 1987; Letnic *et al.*, 2005), modification of predator abundances by human activities (Risbey *et al.*, 2000; Letnic *et al.*, 2009a, b; Moseby *et al.*, 2009) and features of the natural environmental (Read, 1997). For example, on ephemeral islands within Lake Eyre in central Australia, where cats and foxes were absent, house mice (*Mus musculus*) were more than twice as abundant as they were on adjacent mainland areas where cats and foxes were present (Read, 1997). The existence of Australia's largest terrestrial predator, the dingo, also may have positive effects on small mammal populations by reducing the predatory impact of red foxes. In evidence of this, several studies have reported positive relationships between dingoes and the abundance and species richness of small mammals and negative relationships between foxes and dingoes (Read, 1997; Moseby *et al.*, 2006; Letnic *et al.*, 2009a, b). Structurally complex environments, such as rock outcrops, may also provide refuge from predators and so support higher populations of small mammals than surrounding habitats (Burbidge & McKenzie, 1989).

(3) Fire-mosaic model

In a spinifex grassland landscape containing vegetation patches of differing ages after fire, there will be a spatially and temporally dynamic mosaic of distinct habitats that vary in both structure and floristic composition (Burrows & Christensen, 1990; Haydon, Friar & Pianka, 2000). The provision of fire-mosaics in spinifex grasslands results in greater local species diversity, particularly of plants and reptiles (Noble, 1989; Masters, 1996; Pianka, 1996). Several authors have suggested that arid zone mammals may actively exploit the different habitats and resources provided by fire-mosaics (Burbidge *et al.*, 1988; Lundie-Jenkins, 1993; Letnic, 2002, 2004). Others have suggested further that the presence of fire-mosaics may play an important role in facilitating the persistence of arid zone mammal populations, particularly macropodids (Bolton & Latz, 1978; Burbidge *et al.*, 1988; Burbidge & McKenzie, 1989; Flannery, 1994). Fire-mosaics in *Acacia*-dominated shrublands also appear to support more diverse assemblages of small mammals than do homogeneous shrublands, but have been subject to limited research (Dickman *et al.*, 1991).

Post-fire environments provide a community of grasses and herbs more palatable to mammalian herbivores than stands of long-unburnt spinifex (Suijtdorp, 1981; Holm & Allen, 1988; Letnic, 2004). Thus fire-mosaics are thought to offer animals a variety of habitats, including long-unburnt areas with dense spinifex that are suitable for shelter, near to food-rich regenerating areas that are suitable for foraging (Bolton & Latz, 1978; Lundie-Jenkins, 1993). Small mammals certainly utilise fire-mosaics. For example, spinifex hopping mice (*Notomys alexis*) and sandy inland mice (*Pseudomys hermannsburgensis*) have been observed to move through areas regenerating after fire, presumably to feed, but shelter in the dense spinifex of long-unburnt habitats (Letnic, 2002).

Despite observations of mammals exploiting fire-mosaics, however, there is little evidence to suggest that any arid zone

species is dependent on them or that the provision of mixed burnt and unburnt habitats consistently increases species richness or population sizes (Short & Turner, 1994; Letnic & Dickman, 2005). Although some small mammal species such as *Pseudomys desertor* (Letnic, 2003; Kutt, Thurgate & Hannah, 2004) and *Dasykaluta rosamondae* (How & Cooper, 2002) may exhibit strong preferences for long-unburnt habitats (Coventry & Dixon, 1984; Kutt *et al.*, 2004; How & Cooper, 2002; Letnic, 2003), others show no consistent preference for recently burnt or long-unburnt habitats (Masters, 1993; Southgate & Masters, 1996; How & Cooper, 2002; Letnic & Dickman, 2005; Körtner, Pavey & Geiser, 2007). The fire-mosaic model receives little support from reports that small mammal abundance and species richness decrease following wildfires or the fact that no small mammal species shows a consistent preference for recently burnt areas (Coventry & Dixon, 1984; How & Cooper, 2002; Letnic *et al.*, 2005). Taken together, these observations provide little or no quantitative evidence to support the fire-mosaic hypothesis.

V. A STATE-AND-TRANSITION MODEL FOR SMALL MAMMALS OCCUPYING SPINIFEX GRASSLANDS

Our review indicates that small mammal assemblages in the spinifex grasslands of central Australia correlate poorly in terms of both composition and abundance with structural variables indicative of vegetation succession or habitat type (Masters, 1993; Southgate & Masters, 1996; Paltridge & Southgate, 2001; Letnic, 2003). Whereas a few species are associated with dense spinifex habitats (Masters, 1998; Letnic, 2003; Kutt *et al.*, 2004; Letnic & Dickman, 2005), rainfall history, food resource availability and predation pressure appear to be more important factors influencing small mammal assemblages than vegetation structure (Paltridge & Southgate, 2001; Letnic, 2003; Letnic *et al.*, 2005). Similarly, there is little evidence that inter-specific competition is an important factor structuring small mammal assemblages in arid Australia (Morton *et al.*, 1994). Consequently, models of habitat selection based upon inter-specific competition and vegetation structure, such as 'directional' models of post-fire succession (Fox, 1982), appear to offer little insight into the dynamics and structure of mammalian assemblages in Australia's central deserts (Letnic *et al.*, 2004; Letnic & Dickman, 2005).

To help understand small mammal assemblage dynamics and composition in Australia's spinifex grasslands, we introduce a state-and-transition model (*sensu* Westoby, Walker & Noy-Meir, 1989, Fig. 2, Table 1). This model recognises the existence of multiple states of assemblage composition that develop in response to specific environmental conditions, or transitions. It is based largely on empirical studies of mammal populations carried out in the Simpson and Tanami Deserts over many years, but incorporates observations from other spinifex-dominated regions where available. We introduce the model by outlining

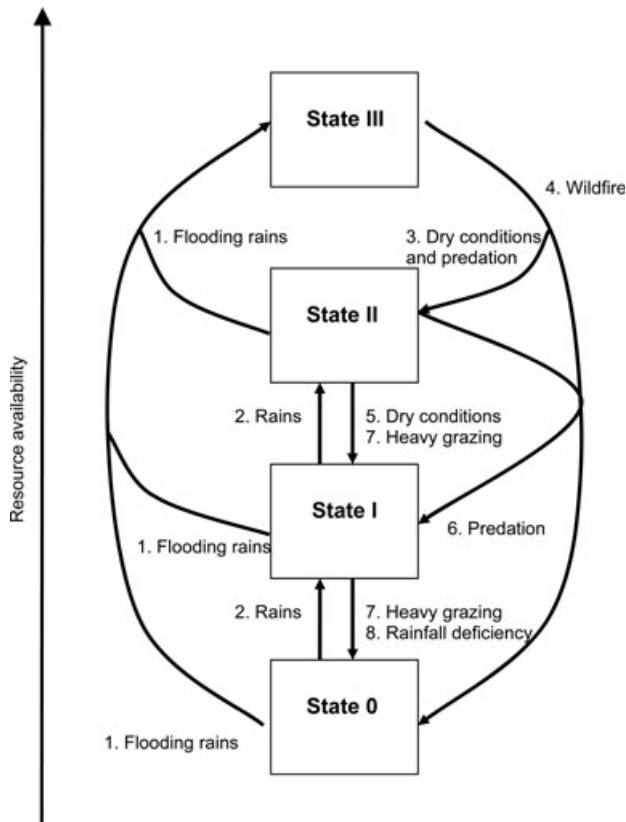


Fig. 2. State-and-transition model proposed to explain small mammal population dynamics in the spinifex grasslands of Australia. See Table 1 for catalogues of state and transitions.

a series of facts or observations about the study populations that we believe are important for understanding both the population and assemblage dynamics. These facts are then incorporated into the conceptual model. We then discuss some potential studies that could be used to test, develop and refine the model that we present.

(1) General elements of the model

(a) Element 1: temporal variability in food resources and the population dynamics of small mammals

In general, the population dynamics of small mammals in arid Australia appear to be determined more by the availability of food resources than by predation, competition or habitat structure (Predavec, 1994a; Mahon, 1999; Predavec, 2000). After rain a pulse of primary productivity and, consequently food resources for small mammals, is triggered, with the size of the pulse proportional to the size of the rainfall event and the availability of soil nutrients (Ludwig *et al.*, 1997).

The ability of mammal species to respond numerically to rainfall events is dependent largely on their reproductive capacity. Native rodents, for example, display highly flexible breeding strategies; they are relatively quick to achieve sexual maturity, are polyoestrous, and can breed year round (Finlayson, 1941; Happold, 1976; Breed, 1992).

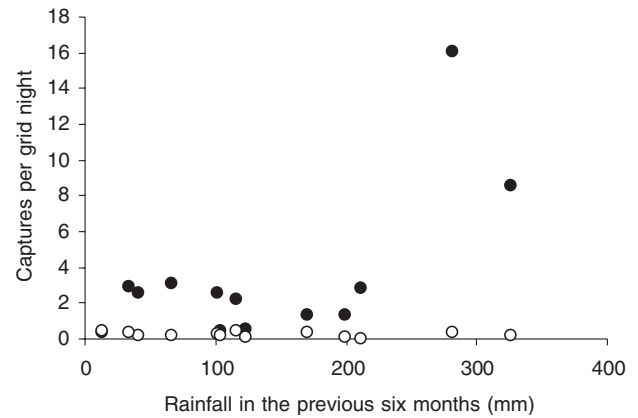


Fig. 3. The relationship between rainfall six months previously and the abundance of native rodents (*Notomys alexis*, *Pseudomys hermannsburgensis* and *P. desertor* combined, filled symbols) and insectivorous dasyurid marsupials (open symbols) in the Simpson Desert between August 1999 and July 2002 (adapted from Letnic *et al.*, 2005). Points are means for separate sampling periods. Rodent numbers increased dramatically following flooding summer rains (>300 mm), while dasyurid numbers remained relatively constant.

Food availability and thus, indirectly, rainfall appears to be the major determinant of their breeding status (Breed, 1979). Dasyurids, by contrast, have relatively inflexible breeding strategies; they are functionally monoestrous in most years and confined to a late winter-spring breeding cycle (Morton, Dickman & Fletcher, 1989; Woolley, 1991; Dickman *et al.*, 2001). During years when conditions are particularly favourable dasyurids may enter oestrus for a second time and produce a second litter (Morton, 1978a; Read, 1984c; Woolley, 1984), but this appears to be rare (Dickman *et al.*, 2001).

The rapid reproductive response of rodents to rainfall-driven resource pulses has been observed to allow rapid increases in population size and expansions of species' ranges (Finlayson, 1939a, b; Plomley, 1972; Newsome & Corbett, 1975; Predavec, 1994a, b; Dickman *et al.*, 1999b). However, rodents do not respond to every fall of rain, and there is some evidence that a threshold level of resource availability or a particular sequence of environmental conditions must occur before populations erupt (Saunders & Giles, 1977; Southgate & Masters, 1996; Dickman *et al.*, 1999b). Quantifying such thresholds is difficult and probably specific to species and geographical localities. For example, in the Simpson Desert, at least 300 mm rain during summer appears to be required to prompt an eruption of the rodents *Pseudomys hermannsburgensis*, *P. desertor* and *Notomys alexis* (Predavec, 1994b; Dickman *et al.*, 1999b; Letnic & Dickman, 2006; Fig. 3). In the case of *Rattus villosissimus* summer rainfall in excess of 500 mm appears required to prompt an eruption in the same area (Predavec & Dickman, 1994; Letnic & Dickman, 2006).

Normally rare species of rodents, such as *P. desertor*, can exhibit startling population increases following large rainfall events (Dickman *et al.*, 1999b; Letnic, 2003). During long

Table 1. Catalogues for the state-and-transition model presented in Fig. 2 for small mammal populations and assemblages inhabiting the spinifex (*Triodia* spp.) grasslands of arid Australia. The information used to construct the three catalogues, for states, transitions, and opportunities and hazards, is based on Newsome & Corbett (1975), Corbett & Newsome (1987), Masters (1993, 1998), Predavec (1994a, b), Predavec & Dickman (1994), Southgate & Masters (1996), Mahon (1999), Dickman *et al.* (1999b, 2001), Paltridge (2002), Letnic (2003, 2004); Letnic *et al.* (2004, 2005), Letnic & Dickman (2005, 2006), Dickman (2006) and Greenville *et al.* (2009)

Catalogue of States (S)	Catalogue of Transitions (T)
<p>S 0. No mammal species is dominant, populations of all species are very low.</p> <p>S I. Assemblage dominated by insectivorous dasyurid marsupials such as <i>Ningauai ridei</i>, <i>Sminthopsis hirtipes</i> and <i>S. youngsoni</i>.</p> <p>S II. Assemblage dominated by the omnivorous rodents <i>Notomys alexis</i> and <i>Pseudomys hermannsburgensis</i>. Insectivorous dasyurids are also common. The carnivorous <i>Dasyercus blythi/cristicauda</i> is uncommon.</p> <p>S III. Assemblage dominated by <i>N. alexis</i>, <i>P. hermannsburgensis</i> and <i>P. desertor</i>. <i>Rattus villosissimus</i>, <i>Leggadina forresti</i> and <i>Mus musculus</i> also may be present. Species richness of insectivorous dasyurids is high, but most species are uncommon; <i>D. cristicauda/blythi</i> is abundant.</p>	<p>T 1. Exceptional summer rains (>90th percentile) stimulate widespread seeding, germination and recruitment of annual and perennial plants, and increased activity of insects. The flush of resources stimulates breeding and allows high recruitment of rodents and the invasion of eruptive species such as <i>R. villosissimus</i>, <i>M. musculus</i> and the red fox (<i>Vulpes vulpes</i>). However, the heavy rains drown or deprive insectivorous dasyurids of shelter resources, thus depleting their populations.</p> <p>T 2. Summer or winter rains within the normal range (>33rd<66th percentile) prompt seeding of annual and some perennial plants. Insect activity increases. Small mammals breed and recruit successfully.</p> <p>T 3. The onset of dry conditions (<33rd percentile) prompts a resource collapse and cessation of breeding by small mammals. Large numbers of terrestrial predators, especially red foxes and feral cats (<i>Felis catus</i>), suppress already declining small mammal populations. Letter-winged kites (<i>Elanus scriptus</i>) are present in large numbers if their primary prey, <i>R. villosissimus</i>, has erupted. This transition is weakened if dingoes (<i>Canis lupus dingo</i>) are present and suppress populations of red foxes and cats, which are the primary predators of small mammals.</p> <p>T 4. Wildfire causes extensive loss of vegetation cover, and greatly increases the risk of predation. In combination with T 3, food shortages also may prevail until the next rains, but restoration of vegetation cover will require many pulse events.</p> <p>T 5. Low rainfall, below the physiologically-effective amount required for widespread germination and growth of annual plants, causes a decline in the seed bank and in the activity or abundance of insects. Breeding and recruitment of small mammals is low. This transition may occur in combination with T 6 and 7.</p> <p>T 6. Predation by feral cats and perhaps goannas (<i>Varanus</i> spp.) reduces population numbers of rodents. Numbers of red foxes have declined as conditions dry, and their predatory impacts are likely to be small.</p> <p>T 7. Intense grazing by introduced herbivores restricts seed production and reduces vegetation cover. Cattle are the major grazers over vast areas of the spinifex grasslands, but feral camels (<i>Camelus dromedarius</i>) also are ubiquitous, and feral donkeys (<i>Equus asinus</i>) and horses (<i>E. caballus</i>) occur patchily. Hard-hooved grazers contribute to soil instability and erosion.</p> <p>T 8. Extreme rainfall deficiency (<10th percentile) results in withering of vegetation, no seed production, and greatly reduced insect activity. In combination with T7, resources for small mammals are reduced to low levels.</p>
Catalogue of Opportunities and Hazards (O/H)	
<p>O/H 1. Periods of high rainfall, often associated with the La Niña phase of the ENSO, are the most critical times for wildlife managers.</p> <p>O/H 2. Following periods of heavy rain, control of introduced predators is required to prevent hyper-predation of native prey populations.</p> <p>O/H 3. Wildfire risk also is greatest after flooding rains when fresh plant growth has died and dried out. Patch burning is needed during the winter months to reduce the extent of spring and summer wildfires.</p> <p>O/H 4. Livestock management is required during dry periods to minimise over-grazing and to prevent the depletion of the food resources of rodents during drought. Culling of feral herbivores may be facilitated by the aggregation of herds at focal watering points.</p>	

low-rainfall periods that can be continent-wide and last for 1–2 years (Kotwicki & Allan, 1998), food availability for rodents decreases rapidly (Predavec, 1994*b*). During these periods, populations of rodents typically undergo steep declines and may even become locally extinct (Newsome & Corbett, 1975; Dickman *et al.*, 1999*b*).

In contrast to rodents, the responses of insectivorous dasyurid marsupial populations to rainfall in arid Australia are quite muted (Fig. 3; Morton, 1978*a*; Friend *et al.*, 1997; Dickman *et al.*, 2001; Bos & Carthew, 2001; Gilfillan, 2001). Although some studies have observed populations of dasyurids to undergo relatively modest increases and possible range expansions following periods of wet conditions (Dickman, Downey & Predavec, 1993*a*; Bos & Carthew, 2001), others have observed populations to show little response to rainfall (Morton, 1978*a, b*; Read, 1984*b, c*) or have even documented population declines (Woolley, 1984, 1990; Dickman *et al.*, 2001; Letnic & Dickman, 2005). It is likely that the dampened response of insectivorous dasyurids to rainfall is a function of their fixed breeding cycle, the reduced availability or stability of their invertebrate food resources (Morton, 1982), and possibly even competition with eruptive species such as rodents or predation from the carnivorous mulgaras (*Dasyercus blythi/cristicauda*).

(*b*) *Element 2: spatial variability in food resources and the mobility of small mammals*

Superimposed on the effects of temporal resource pulsing are the spatial variations in food availability due to localised rains, past fire events, geomorphological features and possibly grazing pressure (Newsome & Corbett, 1975; Morton, 1990; Letnic, 2003). Localised rains, for example, by promoting vegetative growth, seed production and insect activity, can create ephemeral patches of habitat that are rich in food resources (Hunter & Melville, 1994; Letnic & Dickman, 2005). During periods of low food availability such food-rich patches may serve as refuges for small mammal populations (Newsome & Corbett, 1975; Predavec, 2000). Populations of small mammals in refuge habitats are likely to be sustained *in situ* by breeding or by migration (Newsome & Corbett, 1975). Grazing by stock also has the potential to influence food availability for small mammals through decreased seed production and changes in vegetation structure and composition (Ludwig *et al.*, 1997; Letnic, 2004); however, few studies specifically investigating the impact of grazing on small mammals in arid Australia have been conducted (cf. Strong & Low, 1986; James *et al.*, 1995; Letnic 2007).

It is becoming increasingly apparent that the life histories of many central Australian small mammals may be geared more towards locating and exploiting food-rich refuges, that may be transient and widely scattered across the landscape (Dickman *et al.*, 1995; Predavec, 2000; Haythornthwaite & Dickman, 2006*b*), than to exploiting specific habitat types (Letnic *et al.*, 2004; Letnic & Dickman, 2005). Evidence for this comes from observations indicating that central Australian mammals do not display behaviours characteristic of sedentary desert rodents in North America and the

Middle East, such as caching of seeds or, in the case of dasyurids, the construction of permanent burrows (Dickman *et al.*, 1995). Furthermore, many central Australian species show fluctuating habitat preferences (Letnic & Dickman, 2005), utilise habitat mosaics (Letnic, 2002), are nomadic (Read, 1984*b*; Haythornthwaite & Dickman, 2006*b*) and can make nightly movements of a kilometre or more (Letnic, 2002; Haythornthwaite & Dickman, 2006*b*) or longer term movements in the order of several kilometres towards areas that have recently received rainfall (Carstairs, 1976; Read, 1984*b*; Dickman *et al.*, 1995). *Rattus villosissimus*, for example, undergoes large migrations during eruptions (Plomley, 1972; Carstairs, 1976). In the north-eastern Simpson Desert *R. villosissimus*, *Leggadina forresti* and possibly *Sminthopsis macroura* invade the desert dune-fields, apparently traveling more than 10 kilometres from neighbouring Channel Country land-systems during periods of exceptional food availability (C.R. Dickman & M. Letnic, unpublished data).

(*c*) *Element 3: switching trophic cascades and their implications for small mammals*

The rapid numerical responses by small mammal populations to food availability (Predavec, 1994*a*; Letnic, 2003) and of predator numbers to rodent populations (Newsome & Corbett, 1975; Mahon, 1999; Letnic *et al.*, 2005) suggest that the trophic pathways driving small mammal populations in central Australia normally operate from bottom to top (Letnic *et al.*, 2005). However, during boom periods when food is not a limiting resource for any trophic group, typical trophic pathways break down. Periods of high resource availability see increases in mammalian and avian predator populations and subsequently there may be critical levels of predation on small and medium-sized mammals (Letnic *et al.*, 2005; Pavey *et al.*, 2008). Thus ‘top-down’ regulation of small mammal populations by predators appears to be important only during and after rodent eruptions when predators are abundant (Corbett & Newsome, 1987; Mahon, 1999; Letnic *et al.*, 2005). Abundant predators can suppress already declining small mammal populations, particularly if alternative prey such as carrion, locusts or rabbits is available and can maintain the predator populations at high levels (Corbett & Newsome, 1987).

These apparently switching trophic relationships are evident in plots of predator and small mammal abundance before, during and after the La Niña-associated flooding rains experienced in 2000 (Fig. 4). During this period small mammal populations achieved peak numbers in the absence of three species of predators, the dingo, red fox and feral cat. When predators were present there appeared to be an upper limit to small mammal abundance, suggesting the existence of top-down regulation (Letnic *et al.*, 2005). In arid areas where dingoes are rare or extinct and meso-predators such as the red fox and feral cat are the dominant carnivores, top-down predation is likely to be an even stronger force shaping small mammal assemblages because of the predilection of meso-predators for small prey (Read, 1997; Moseby *et al.*, 2006; Letnic *et al.*, 2009*a, b*).

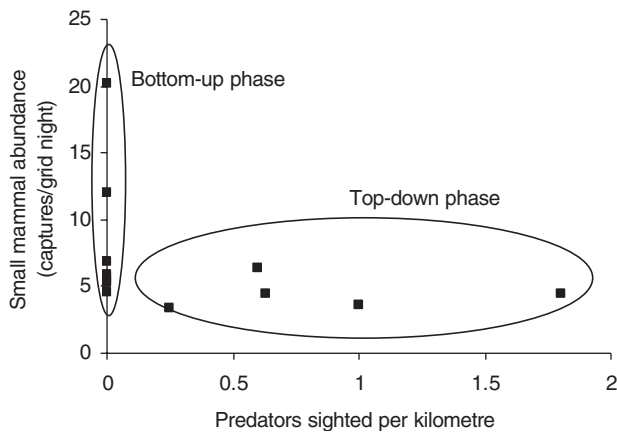


Fig. 4. The relationship between the abundance of predators (combined sightings of dingoes, foxes and cats) and small mammals (all species with body mass <100 g) in the Simpson Desert between August 1999 and July 2002 (modified after Letnic *et al.*, 2005). Points are means for separate sampling periods. Small mammals reached their peak abundance in the absence of predators. When predators were present there appears to be an upper limit to small mammal abundance, suggesting the existence of top-down regulation.

During periods of high predator activity or abundance it is likely that habitat structure is an important influence on small mammal assemblages (Letnic *et al.*, 2005). During periods of low predator abundance few small mammal species exhibit strong habitat preferences (Kotler, Dickman & Brown, 1998; Haythornthwaite & Dickman, 2000; Körtner *et al.*, 2007), suggesting that risk of predation (Kotler, Brown & Mitchell, 1994) has little effect on their habitat selection at these times. Fluctuating habitat preferences by small mammals and the use of habitat mosaics suggest that some species, such as *P. hermannsburgensis*, *N. alexis* and *Sminthopsis youngsoni*, may normally select habitat in response to food availability rather than predation risk (Letnic, 2003; Letnic & Dickman, 2005). However, during periods of high predator abundance, populations of these small mammals are often more closely associated with dense spinifex habitats, where presumably the grass hummocks offer shelter from predation (Letnic *et al.*, 2005).

In pastoral areas, livestock may further influence the trophic relationships of small mammals (Hayward, Heske & Painter, 1997). Firstly, large herbivores can directly limit the production of herbage and seeds (Letnic, 2004) and consequently remove food resources that would be otherwise available for smaller mammals. This is likely to impose constraints on food resources throughout all stages of the pulse-resource cycle. Secondly, herbivores often simplify or degrade habitat structure by defoliation and trampling (Eccard, Wather & Milton, 2000; Read, 2002; Letnic, 2004). Thus grazers may increase the exposure of small mammals to their predators by reducing the amount of available cover. In these situations small mammals seldom erupt despite strong pulses of primary productivity (Read, 1984*a, c*; Dickman *et al.*, 1993*b*).

(2) Synthesis of the model

Our conceptual model (Fig. 2, Table 1) recognises the existence of multiple states of small mammal assemblages that develop in response to sets of 'transitions'. The transitions between states are prompted by conditions such as natural events or management strategies that influence assemblage composition by affecting food resources and population dynamics. To construct a state-and-transition model the following information is required (see Westoby *et al.*, 1989): (1) a catalogue of all possible assemblage states; (2) a catalogue of possible transitions from one state to another; and (3) a catalogue of opportunities/hazards. This information is presented and explained in Table 1.

Alternative assemblages or 'states' are often thought to arise from changes in environmental conditions that shift species densities from one equilibrium point towards another (Noy-Meir, 1975; May, 1977; Petraitis & Latham, 1999). Throughout central Australia subtle changes in resource abundance owing to rainfall, and possibly grazing, can result in gradual changes in small mammal assemblages that are expressed as shifts in species abundance and dominance (Letnic *et al.*, 2004). However, exceptional rainfalls, high predation pressure and wildfire also can result in swift and apparently discontinuous changes in assemblage structure. In the case of exceptional rainfalls these rapid changes result from explosive breeding and the migration of species following large pulses of primary productivity. High levels of predation, on the other hand, can result in the precipitous decline of small mammal populations, particularly those of rodents and the mulgara (Dickman *et al.*, 1999*b*; Letnic *et al.*, 2005).

Previous studies have emphasised the importance of identifying whether alternative states are stable and self-replicating (Connell & Sousa, 1983; Dublin, Sinclair & McGlade, 1990; Petraitis & Latham, 1999). However, herein we emphasise the importance of recognising multiple states and focus not on whether the states are stable but rather on the environmental conditions (transitions) that prompt changes between them. The reasons for this are twofold. Firstly, field studies suggest that some assemblages (State III, see Fig. 2) are likely to be short-lived, or unstable, owing to the existence of high predation pressure. Despite this expectation, State III assemblages are not always short-lived; for example, Predavec (1994*a*) documented a rodent eruption that was sustained at State III conditions for two years. Secondly, our model is intended primarily as an interpretive and explanatory tool that should assist with the implementation of management strategies in response to prevailing or predicted environmental conditions, and not necessarily as a theoretical construct.

Finally, the state-and-transition model proposed by Westoby *et al.* (1989) was envisaged originally to describe a single piece of ground over time. However, our model can be conceptualised both as a descriptor of temporal variation in assemblage structure or as a geographical map that describes spatial variation among small mammal assemblages (Letnic *et al.*, 2004). Used in this way, the model captures the two

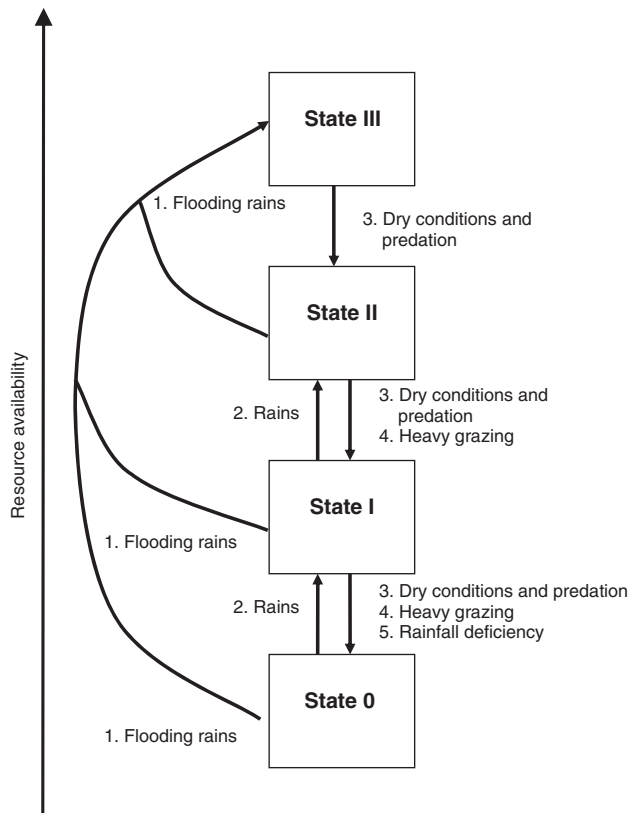


Fig. 5. State-and-transition model explaining the population and assemblage dynamics of small mammals in the cracking soil landscapes of the southern Lake Eyre Basin of Australia. See Table 2 for catalogues of states and transitions.

key aspects of variation in resource pulses that characterise the spinifex grassland environment.

(3) Testing the model

An important aspect of state-and-transition models is that they can be augmented or modified as further information is garnered and research is undertaken to test hypotheses or generate new information on assemblage states and transitions (Westoby *et al.*, 1989). The model presented here should thus be viewed only as a conceptual starting point, with future research being necessary to refine and improve it further. Several approaches could be taken to do this, but we suggest that studies testing the transitions between assemblage states and empirically validating the existence of alternative states be given priority (Petraitis & Latham, 1999). These studies should include:

- (1) Surveying different spinifex deserts to confirm that the states identified here, using data largely from the Simpson and Tanami Deserts, are generally recognisable. We predict that, whereas the identity of small mammal species will vary in different regions of the spinifex grassland biome, assemblages corresponding to the four states characterised

in Table 1 will be detectable. Defining different assemblages of species as alternative community states is rarely a clear-cut exercise and is clouded by the difficulties of defining or distinguishing assemblages in the variable natural world (Connell & Sousa, 1983; Petraitis & Latham, 1999). Connell & Sousa (1983) suggested that, to be considered alternative states, each assemblage must be able to persist for at least one generational turnover of the dominant species. In our model, it needs to be established if the states, defined by the relative abundances of species, are sufficiently long-lived or distinct to be useful in describing assemblage dynamics for land managers who are concerned with implementing real-time management strategies. Further research addressing the validity or appropriateness of the alternative states is thus a primary recommendation.

- (2) Long-term monitoring to establish thresholds in rainfall and other resources that prompt transitions between states. Such studies could be used to estimate the probabilities of occurrence of shifts between states, and of events such as wildfire, increases in predator activity, rodent eruptions and rainfall extremes. Complementary to these studies would be the development of contingency plans for wildlife management. In arid Australia, such contingencies are likely to include poison-baiting campaigns for introduced predators and prescribed burning to reduce the likelihood of broadscale wildfires.
- (3) Establishing the role that trophic cascades have in determining assemblage composition. For example, water or nutrients could be supplemented to simulate Transition 1 (rainfall) and to experimentally establish threshold resource levels for the existence of alternative states. Predator-removal experiments and food manipulations could be conducted when State III assemblages occur to determine the relative importance of Transition 3 processes (food resources, predation), and possibly other factors, in driving the shift from State III to State II assemblages. Experimental identification of the processes responsible for the decline of wildlife populations could then be used to develop specific management strategies aimed at mitigating the impact of threatening processes (Caughley, 1994; Dickman, 1996b).
- (4) Testing the potential for interactions between resource levels, grazing by large herbivores, and assemblage structure. It is likely that large herbivores such as kangaroos and livestock compete with small mammals for food (Letnic, 2004), and that both removal of herbage and soil compaction will detrimentally affect small mammals by altering habitat structure (Morton, 1990; Dickman *et al.*, 1993b). Excessive grazing pressure has been commonly identified as a widespread threat to wildlife in arid Australia (Morton, 1990; Lunney, 2001; Letnic, 2007), however, few studies have

Table 2. Catalogues for the state-and-transition model presented in Fig. 5 for small mammal populations and assemblages inhabiting the cracking clay soils of the southern Lake Eyre Basin of arid Australia. The information used to construct the three catalogues, for states, transitions, and opportunities and hazards, is based on Finlayson (1939*b*), Plomley (1972), Brandle & Moseby (1999) and Letnic *et al.* (2009*b*). The model incorporates drought, predator and livestock refuges, respectively. These refuges are conceptualized as being spatially distinct patches in the landscape where alternate states exist due to higher primary productivity, reduced predation by introduced predators and the absence of grazing by livestock, respectively

Catalogue of States (S)	Catalogue of Transitions (T)
<p>Drought refuge. Secondary drainage channels have higher availability of nutrients and moisture and act as drought refugia. Assemblage dominated by eruptive rodents such as <i>Pseudomys australis</i> and <i>Mus musculus</i>. <i>Rattus villosissimus</i>, <i>Leggadina forresti</i> and some dasyurid marsupials may also be present.</p> <p>Predator and livestock refuge. Predators and livestock are scarce in areas distant from artificial water, allowing for higher small mammal populations than in areas near water.</p> <p>S 0. No small mammal species is dominant, populations of all species are very low, and rodents are restricted to drought or predator and livestock refugia.</p> <p>S I. Assemblages are dominated by insectivorous dasyurid marsupials, particularly <i>Planigale</i> and <i>Sminthopsis</i> spp. Rodent populations are small and localised.</p> <p>S II. Native rodents dominate, and dasyurid marsupials are common.</p> <p>S III. During wet periods assemblages are dominated by eruptive rodents. <i>Pseudomys australis</i> may be abundant, and <i>M. musculus</i> is often present in very large numbers.</p>	<p>T 1. Exceptional summer rains (>90th percentile) stimulate widespread seeding, germination and recruitment of annual and perennial plants. The flush of resources allows high recruitment of rodents, especially invasive <i>M. musculus</i>, and also strong numerical responses by red foxes (<i>Vulpes vulpes</i>) and feral cats (<i>Felis catus</i>).</p> <p>T 2. Summer or winter rains within the normal range (>33rd < 66th percentile) prompt seeding of annual and perennial plants. Insect activity increases. Small mammal recruitment is successful.</p> <p>T 3. Dry conditions prompt a resource collapse. Terrestrial predators, especially red foxes and cats, suppress already declining small mammal populations.</p> <p>T 4. Intense grazing by livestock, rabbits and kangaroos restricts seed production and reduces vegetation cover.</p> <p>T 5. Rainfall deficiency results in withering of vegetation. No seed production, insect resources are scarce. Grazing contributes to vegetation loss and soil instability.</p>
Catalogue of Opportunities and Hazards (O/H)	
<p>O/H 1. As for the spinifex grasslands (Table 1, Fig. 2), high rainfall periods are critical times for wildlife managers. Following periods of heavy rain, predator control is especially important to prevent hyper-predation on native prey populations.</p> <p>O/H 2. Fox and cat populations are buffered by abundant rabbits and so remain as constant threats to small mammals. Rabbits are confined locally to refuge habitats during very dry periods, thus providing opportunities to control their populations and hence also reduce the impacts of foxes and cats.</p> <p>O/H 3. Livestock management is required during dry periods to minimise over-grazing and to prevent the depletion of the food resources of rodents during drought.</p>	

addressed the impact of grazing on small mammals empirically (James *et al.*, 1995; Frank *et al.*, 2008).

VI. MODELS FOR OTHER HABITATS

Studies of small mammal population dynamics from other arid habitats suggest that the main elements of our model for the spinifex grasslands are likely to be broadly applicable. For example, native rodents generally exhibit much greater amplitude in population size than do sympatric dasyurids, although both groups appear responsive to rainfall-driven variations in the timing and location of food resources (Finlayson, 1939*a, b*, 1941; Read, 1984*b, c*; Brandle, 1998). There is also some evidence of the deleterious impacts of predators (Finlayson, 1939*b*; Pavey *et al.*, 2008; Letnic *et al.*, 2009*b*) and of overgrazing by livestock (Frank & Soderquist, 2005) in non-spinifex biomes.

The most extensive data from non-spinifex habitats come from the cracking soil landscapes of the Lake Eyre Basin

and from localised pockets of these soils further east. In the southerly parts of this region landscapes are diverse and dominated by tracts of shrubland, tussock grassland or sparsely vegetated stony downs. Secondary drainage channels accumulate nutrients and support taller trees and shrubs. Much of the region is subjected to grazing by livestock and degradation by rabbits, and introduced predators are often numerous; house mice may achieve large numbers locally (Brandle, 1998; Letnic *et al.*, 2009*b*). Vegetation is usually too sparse to carry wildfires, even after heavy rains have stimulated the growth of annual and perennial grasses. The impacts of foxes and rabbits appear to have been greater in the southern parts of the Lake Eyre Basin, and accordingly carnivorous dasyurid marsupials and large rodents (>50 g) are rare or absent (Watts & Aslin, 1974; Robinson *et al.*, 2000). Because of these differences we present separate models for the southern (Fig. 5, Table 2) and north-eastern (Channel Country) parts of the Lake Eyre Basin (Fig. 6, Table 3). Due to the general absence of fire, the state-transition models for the cracking soils of the Lake Eyre

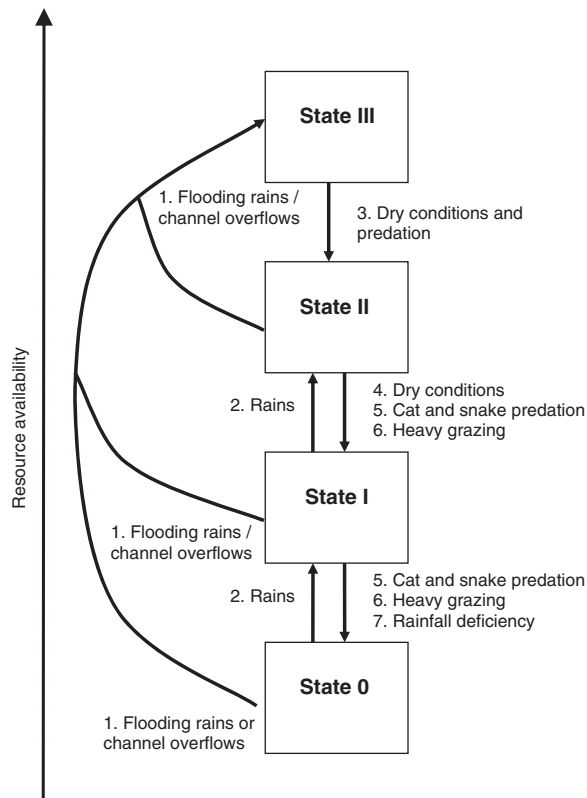


Fig. 6. State-and-transition model explaining the population and assemblage dynamics of small mammals in the Channel Country of Australia. See Table 3 for catalogues of states and transitions.

Basin are somewhat simpler than the model for the spinifex grasslands.

In the Channel Country region of the north-eastern Lake Eyre Basin landscapes are dominated by sparse gibber plains with cracking soils. These are intersected by networks of primary and secondary drainage channels that support corridors of vegetation. Wildfires occur very rarely. Rabbits are rare in the northern parts of the Basin and cattle are grazed at low densities of 1–5 per km² (Wilson, Purdie & Ahern, 1990). Red foxes also are scarce or absent, although feral cats are common at times (Pettigrew, 1993; Letnic *et al.*, 2009b). Heavy summer rains in the Channel Country stimulate eruptions of *Rattus villosissimus*, other native rodents, and also larger carnivorous dasyurids such as the kowari *Dasyuroides byrnei* (Cleland, 1918; Crombie, 1944; Watts & Aslin, 1974; Lim, 1992). In contrast to the more southerly regions of the Basin, such eruptions in the Channel Country can be driven by flooding caused by rainfall that has fallen further north rather than just by on-site rainfall. Assemblage states in the Channel Country are similar to those in the south of the Lake Eyre Basin, but some differences are apparent in the transitions prompting shifts from one state to another (Fig. 6, Table 3). These reflect differences in grazing pressure, the presence or abundance of introduced mammals, and the prominence of snakes as small mammal predators.

In the southern arid zone where most rainfall occurs in winter there are extensive tracts of chenopod shrublands dominated by low (<2 m high) perennial shrubs of the genera *Atriplex* and *Maireana*. Sheep and to a lesser extent cattle grazing are the dominant land uses (Harrington *et al.*, 1984) and rabbits, house mice and foxes are common (Read & Bowen, 2001; Moseby *et al.*, 2009). There have been widespread losses of native rodents throughout the chenopod shrublands presumably due to predation by introduced predators and habitat degradation by herbivores including livestock, rabbits and kangaroos (Dickman *et al.*, 1993b; Moseby *et al.*, 2009). Fires occur rarely. The model for the chenopod shrublands (Fig. 7, Table 4) differs from the models presented for the spinifex grasslands and the cracking soils of the Lake Eyre Basin because it does not include a State 0 assemblage. The reason for this is that literature from the region suggests that dasyurid marsupials are present during drought (Read, 1992; Moseby *et al.*, 2009).

The state-and-transition model for chenopod shrublands (Fig. 7, Table 4) shows that resource pulses emanating from heavy rainfalls can prompt eruptions of native rodents and introduced house mice and that predation, herbivory and drought can also influence the composition of mammal assemblages. However, field studies conducted in these environments demonstrate that population increases of native rodents following resource pulses are dampened in the presence of introduced predators and rabbits, and the effects of predators can also be detected during drought (Moseby *et al.*, 2009). These observations provide strong evidence for the existence of predation refuges. Consequently, we have incorporated a predation refuge as an alternate state in the catalogue for the state-and-transition model for this landscape.

The state-and-transition models proposed here assume that there are unifying principles that can be applied to small mammal assemblages throughout arid Australia. However, the models are not meant to provide definitive descriptions of the processes determining mammal assemblages in each habitat but are presented more as starting points to describe the environmental forces shaping assemblages and as prompts for future studies. Due to differences in climate, soils, land-use practice and species distributions, both assemblage states and the transition events that prompt shifts between them are likely to differ between localities and regions. Indeed, recent surveys in different habitat types in Western Australia suggest that large differences in assemblages and models remain to be described (e.g. How & Cooper, 2002; Thompson & Thompson, 2008). Thus, further use of the conceptual framework presented here will need to be tailored to describe adequately mammalian dynamics in other landscapes.

VII. APPLICATIONS OF THE STATE-AND-TRANSITION MODEL

Arid Australian habitats have experienced considerable changes since the onset of European settlement, and have

Table 3. Catalogues for the state-and-transition model presented in Fig. 6 for small mammal populations and assemblages inhabiting the cracking gibber soil plains of the Channel Country of arid Australia. The information used to construct the three catalogues, for states, transitions, and opportunities and hazards, is based on Cleland (1918), Finlayson (1939*a, b*, 1941), Crombie (1944), Mack (1961), Watts & Aslin (1974), Carstairs (1976), Lim (1992), McFarland (1992), Pettigrew (1993), Brandle (1998), McRae (2004), Pavey *et al.* (2008) and Letnic *et al.* (2009*b*)

Catalogue of States (S)	Catalogue of Transitions (T)
<p>S 0. No mammal species is dominant, populations of all species are very low.</p>	<p>T 1. Exceptional on-site summer rains (>90th percentile) or extensive overflowing of drainage channels from rains further north stimulate widespread seeding, germination and recruitment of annual plants and geophytes, as well as woody perennial plants along drainages, and increased activity of insects. These resources stimulate breeding and recruitment of rodents and the invasion from drainage channels of eruptive species such as <i>R. villosissimus</i> and <i>M. musculus</i>. Feral cat (<i>Felis catus</i>) and dingo (<i>Canis lupus dingo</i>) populations increase, as do populations of avian predators such as diurnal black kites (<i>Milvus migrans</i>), nocturnal letter-winged kites (<i>Elanus scriptus</i>) and barn owls (<i>Tyto alba</i>). Red foxes (<i>Vulpes vulpes</i>) are very rare in the region, but may increase locally if present. The heavy rains drown or deprive insectivorous dasyurids of shelter resources, thus depleting their populations.</p>
<p>S I. Assemblage dominated by insectivorous dasyurid marsupials such as <i>Planigale gilesi</i>, <i>P. tenuirostris</i> and <i>Sminthopsis crassicaudata</i> and <i>S. macroura</i>.</p>	<p>T 2. Summer or winter rains within the normal range (>33rd < 66th percentile) prompt seeding of annual and some perennial plants. Insect activity increases. Small mammals breed and recruit successfully.</p>
<p>S II. Assemblage dominated by omnivorous rodents such as <i>Notomys cervinus</i>, <i>Pseudomys hermannsburgensis</i> and <i>Leggadina forresti</i>. Insectivorous dasyurids are also common. The carnivorous dasyurid marsupial <i>Dasyuroides byrnei</i> is present but uncommon.</p>	<p>T 3. The onset of dry conditions (<33rd percentile) drives a resource collapse and cessation of breeding by small mammals. Large numbers of terrestrial predators, especially feral cats and birds of prey, suppress already declining small mammal populations. Dingoes, if present, consume small rodents but may slow this transition if they impact negatively on the activity of feral cats.</p>
<p>S III. Assemblage dominated by highly abundant <i>Rattus villosissimus</i>, with <i>N. cervinus</i>, <i>P. hermannsburgensis</i>, <i>P. australis</i> and <i>L. forresti</i> also common. If <i>Mus musculus</i> occurs, it is very abundant. Species richness, but not abundance, of insectivorous dasyurids is high; <i>D. byrnei</i> is abundant.</p>	<p>T 4. Low rainfall, below the physiologically-effective amount required for widespread germination and growth of annual plants, and drying of channel overflow areas, causes a decline in the seed bank and in the activity or abundance of insects. Breeding and recruitment of small mammals are low. This transition may occur in combination with transitions 5 and 6.</p> <p>T 5. Predation by feral cats, inland taipans (<i>Oxyuranus microlepidotus</i>), other large elapid snakes (<i>Pseudechis</i> spp., <i>Pseudonaja</i> spp.) and pythons (largely <i>Aspidites melanocephalus</i> and <i>A. ramsayi</i>) reduces population numbers of rodents.</p> <p>T 6. Intense grazing by cattle restricts seed production and reduces vegetation cover. Feral donkeys (<i>Equus asinus</i>), horses (<i>E. caballus</i>) and feral pigs (<i>Sus scrofa</i>) will, if present, contribute to resource depletion for small mammals, as will red kangaroos (<i>Macropus rufus</i>).</p> <p>T 7. Extreme rainfall deficiency (<10th percentile) withers annual vegetation, stops growth and seed production of perennial plants, and greatly reduces insect activity. In combination with transitions 5 and 6, populations of small mammals are reduced to low levels.</p>
Catalogue of Opportunities and Hazards (O/H)	
<p>O/H 1. Periods of high rainfall or flooding are critical times for wildlife managers.</p>	
<p>O/H 2. Following moisture-driven pulses of productivity, control of feral cats is most important to prevent hyper-predation of small mammal populations. Cats shelter in trees and shrubs along drainage channels during drought, concentrating their activity and thus allowing effective opportunities for control at this time.</p>	
<p>O/H 3. Livestock management is required during dry periods to minimise over-grazing in drainage channels, which likely provide key food and shelter resources for native rodents during drought. Culling of feral herbivores may be facilitated at this time as animals congregate along drainage channels and at focal watering points.</p>	

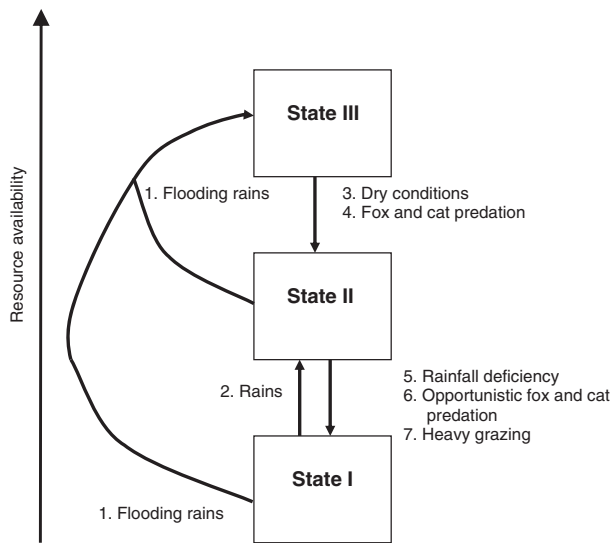


Fig. 7. State-and-transition model explaining the population and assemblage dynamics of small mammals in the chenopod shrublands of the southern arid zone of Australia. See Table 4 for catalogues of states and transitions.

suffered very high rates of loss of small and medium-sized native mammals (Morton & Baynes, 1985; McKenzie *et al.*, 2007). Effective management of the species that remain is imperative, both to conserve the species themselves and to retain their ecological functions (Dickman *et al.*, 1993b; Martin, 2003). We suggest that the state-and-transition model framework provides a useful way forward for managers. Thus, knowledge of rainfall conditions, fire danger and, when information is available, stocking rates, can be used to predict likely changes in assemblage composition and when to implement different management strategies.

In the Simpson Desert, for example, where most of the foundation data for this review were derived, the most critical periods for conservation managers follow flooding rains (see Fig. 2, Table 1). The rains stimulate a surge in primary productivity and thus greater fuel loads to sustain wildfires when the green growth has died back (Greenville *et al.*, 2009). Following the transition to State III conditions when native small mammals are abundant, introduced predators increase dramatically and can assist in driving small mammal populations to the very low abundances characteristic of State I. To ameliorate the acute threats posed by wildfire and hyper-predation, managers could profitably burn small strips of vegetation to provide break points for large fires, and control predators before their numbers build up. Both management interventions would take place ideally six months to a year after flood rains had fallen and before Transitions 3 and 4 could take effect (Fig. 2).

In the Channel Country, by contrast, fire does not appear to be an important transition (Fig. 6; Table 3). However, during State III conditions, predation may be a critical factor influencing wildlife assemblages. By providing abundant prey for predators, eruptions of *R. villosissimus* and other rodents can sustain high populations of avian, reptilian

and mammalian predators (Plomley, 1972; Pettigrew, 1993; Letnic & Dickman, 2006) and thus have the potential to threaten other fauna *via* apparent competition (Sinclair *et al.*, 1998). To reduce the likelihood of transitions 3 and 5 taking effect, control of introduced mammalian predators could be undertaken before predator numbers build up. Because increases in mammalian predator populations typically lag 9–15 months behind those of rodent populations (Plomley, 1972), managers should have ample opportunity to plan and implement predator control activities.

As the climate of the Earth changes in response to global warming (Easterling *et al.*, 2000; Hughes, 2003), arid areas are likely to experience even higher temperatures in future, as well as reduced rainfall and fewer but more extreme flooding events (Easterling *et al.*, 2000). As a consequence, resource pulses may be expected to occur less frequently but be greater in magnitude when they occur (Huxman *et al.*, 2004). Applying state-and-transition model frameworks may be useful to predict how ecosystems will respond to climatic variations including global warming. For example, using the state-and-transition model for the hummock grasslands (Table 1, Fig. 2), we predict that an increase in the frequency and amplitude of resource pulses will promote an increase in the intensity and geographical extent of wildfires. To conserve the habitat of small mammals and reduce their exposure to predation, management intervention, using small-scale control burns, would then be required less often but would become even more important to implement in the wake of rare flood rains.

VIII. CONCLUSIONS

- (1) Local and especially flooding rains are key drivers of productivity in arid Australian landscapes, stimulating the growth of annual herbs and grasses and perennial shrubs. These pulses are often localised in space and time, but they provide key food resources that stimulate population eruptions of consumer organisms. Small mammals such as rodents exploit the surges in primary production directly, whereas small marsupials exploit the more delayed bursts of secondary production by preying upon rodents or invertebrates. The resource pulses drive dramatic shifts in both the population dynamics and assemblage composition of small mammals in arid Australia.
- (2) Post-rain declines in primary productivity reduce rates of increase of small mammals and drive population declines. However, declines may be hastened in many arid regions by heavy losses to introduced predators such as foxes and cats; local extinctions may result if the predators can maintain their populations by switching to alternative prey such as rabbits or reptiles as the smaller mammals become scarce. Over-grazing by kangaroos and domestic stock also depletes food and shelter resources and may expose small mammals to greater risks of predation, speeding population declines

Table 4. Catalogues for the state-and-transition model presented in Fig. 7 for small mammal populations and assemblages inhabiting the chenopod shrublands of arid southern Australia. The information used to construct the three catalogues, for states, transitions, and opportunities and hazards, is based on Read (1984*a, b, c*), Read (1992), Moseby & Read (1999), Read *et al.* (1999), Read & Bowen (2001), Holden & Mutze (2002), Read & Wilson (2004) and Moseby *et al.* (2009). The model incorporates drought and predator refuges, respectively. These refuges are conceptualized as being spatially distinct patches in the landscape where alternate states exist due to higher primary productivity and reduced predation by introduced predators, respectively

Catalogue of States (S)	Catalogue of Transitions (T)
Drought refuge. Low-lying drainage areas provide productive and relatively complex sites in the landscape. Assemblage dominated by <i>Sminthopsis crassicaudata</i> and <i>Mus musculus</i> . Other rodents including <i>Pseudomys bolami</i> , <i>P. desertor</i> and <i>Leggadina forresti</i> may be present.	T 1. Exceptional summer rains (>90th percentile) stimulate widespread seeding, germination and recruitment of annual and perennial plants. The flush of resources allows for high recruitment of rodents such as <i>M. musculus</i> and <i>P. bolami</i> and, where present, <i>N. alexis</i> .
Predator refuge. Control of introduced predators releases native rodents from predation by introduced cats and red foxes. Insectivorous dasyurids are also common.	T 2. Summer or winter rains within the normal range (>33 rd <66 th percentile) prompt seeding of annual and some perennial plants. Insect activity increases. Small mammals breed and recruit successfully.
S I. Assemblage dominated by insectivorous dasyurid marsupials and <i>M. musculus</i> .	T 3. In the absence of introduced predators dry conditions prompt a resource collapse and the slow decline of mammal populations.
S II. Assemblage dominated by omnivorous rodents, <i>M. musculus</i> and <i>P. bolami</i> . Insectivorous dasyurids are also common. <i>Notomys alexis</i> , <i>L. forresti</i> and <i>P. desertor</i> may be present.	T 4. Together with T 3, sustained predation by large numbers of red foxes (<i>Vulpes vulpes</i>) and feral cats (<i>Felis catus</i>) suppress already declining small mammal populations. Small mammals are the primary prey items of foxes and cats.
S III. Assemblage dominated by the omnivorous rodents <i>Notomys alexis</i> , <i>M. musculus</i> and <i>P. bolami</i> . Insectivorous dasyurids are common, and <i>L. forresti</i> and <i>P. desertor</i> are present.	T 5. Extreme rainfall deficiency (<10 th percentile) results in withering of vegetation, no seed production, and greatly reduced insect activity. In combination with T 7, resources for small mammals are reduced to low levels. In further combination with T 6, these transitions can suppress small mammals to critically low levels outside refuge areas.
	T 6. Occasional predation by red foxes and feral cats reduces population numbers of rodents. Foxes and cats exhibit prey switching in this system and primarily consume rabbits, reptiles and carrion when small mammal populations are low.
	T 7. Intense grazing by herbivores restricts seed production and reduces vegetation cover. Sheep, rabbits and kangaroos are the major grazers. Hard-hooved grazers contribute to soil instability and erosion.
Catalogue of Opportunities and Hazards (O/H)	
O/H 1. Fox and cat populations are buffered through dry periods by preying upon reptiles and rabbits and consuming carrion from kangaroo and livestock carcasses. Thus fox and cat predation is a constant threat to small mammal populations throughout all stages of the resource cycle.	
O/H 2. Livestock management is required during dry periods to minimise over-grazing and to prevent the depletion of the food resources of rodents during drought.	

still further. Faunal collapse occurs after long periods of rainfall deficiency.

- (3) Equilibrium models cannot adequately capture the dynamics of species populations and assemblages in such variable resource-pulse systems, as population regulation does not occur. However, state-and-transition models explicitly incorporate the effects of intermittent resource pulses. They incorporate the existence of multiple states of population size and assemblage composition, and can provide useful descriptors of small mammal assemblages in arid environments. Because different states develop in response to specific environmental conditions such as rainfall and predation, models can be used to predict the dynamics of assemblages in both time and space

and should allow more informed management of small mammals and their habitats in Australia. These model frameworks will likely be suitable for application in other regions where mammals erupt in response to resource pulses, and should find application also in informing best-practice management in response to climate change.

- (4) Future research might profitably seek to test the generality of our state-and-transition models in other spinifex-dominated regions and other arid biomes. It should also evaluate the robustness of the states that we have defined here, on the basis of the relative abundance and composition of species that are present, and explore whether alternative states can be identified. As other organisms are likely to

respond to resource pulses, it will be of heuristic interest and practical benefit to determine if their dynamics can be described and predicted by state-and-transition models, and if these are compatible with those for mammals. Birds and reptiles are obvious candidate groups for study among the vertebrates (Dickman *et al.*, 1999a; Kingsford *et al.* 1999a, b), as are insects and spiders among the invertebrates (Duncan & Dickman, 2001; Langlands, Brennan & Pearson, 2006).

- (5) Finally, experimental manipulations and long-term monitoring are needed to identify the transitions that cause shifts between states, to document whether thresholds need to be achieved to prompt state-shifts, and also to quantify whether transitions act in additive or interactive ways. The most obvious such interactions in the spinifex grasslands relate currently to the effects of wildfire and grazing in reducing vegetation cover, and the consequently increased risks of predation that small mammals face in these newly exposed environments. As extreme climatic events such as floods and wildfires are predicted to be more severe and frequent in future, and will likely have disruptive effects on species interactions (Thibault & Brown, 2008), understanding how transitions cause state-changes should be a current research priority.

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X. REFERENCES

- AHUJA, A. (2005). Scenario of clinical studies of cutaneous leishmaniasis of humans and canines. In: *Changing faunal ecology in the Thar Desert*. (eds B. K. TYAGI & Q. H. BAQRI), pp. 305–322. Scientific Publishers, Jodhpur.
- ANDREW, D. L. & SETTLE, G. A. (1982). Observations on the behaviour of species of *Planigale* (Dasyuridae, Marsupialia) with particular reference to the narrow-nosed planigale (*Planigale tenuirostris*). In: *Carnivorous marsupials*. (ed. M. ARCHER), pp. 311–324. Royal Zoological Society of New South Wales, Sydney.
- AUMANN, T. (2001). Habitat use, temporal activity patterns and foraging behaviour of raptors in the south-west of the Northern Territory, Australia. *Wildlife Research* **28**, 365–378.
- BENNETT, K. H. (1887). Notes on a species of rat (*Mus tomponii*, Ramsay) now infesting the western portion of N.S.W. *Proceedings of the Linnean Society of New South Wales* **2**, 447–449.
- BLACKWELL, G. L., POTTER, M. A., MCLENNAN, J. A. & MINOT, E. O. (2003). The role of predators in ship rat and house mouse eruptions: drivers or passengers? *Oikos* **100**, 601–613.
- BOLTON, B. L. & LATZ, P. K. (1978). The western hare-wallaby, *Lagorchestes hirsutus* (Gould) (Macropodidae), in the Tanami Desert. *Australian Wildlife Research* **5**, 285–293.
- BOS, D. G. & CARTHEW, S. M. (2001). Population ecology of *Ningau yvonneae* (Dasyuridae: Marsupialia) in the Middleback Ranges, Eyre Peninsula, South Australia. *Wildlife Research* **28**, 507–515.
- BOUGET, C. & DUELLI, P. (2004). The effects of windthrow on forest insect communities: a literature review. *Biological Conservation* **118**, 281–299.
- BRADSHAW, D. (2003). *Vertebrate ecophysiology: an introduction to its principles and applications*. Cambridge University Press, Cambridge.
- BRANDLE, R., ed. (1998). *A biological survey of the stony deserts, South Australia, 1994–1997*. Department for Environment, Heritage and Aboriginal Affairs, Adelaide.
- BRANDLE, R. & MOSEBY, K. E. (1999). Comparative ecology of two populations of *Pseudomys australis* in northern South Australia. *Wildlife Research* **26**, 541–564.
- BREED, W. G. (1979). The reproductive rate of the hopping mouse *Notomys alexis* and its ecological significance. *Australian Journal of Zoology* **27**, 177–194.
- BREED, W. G. (1992). Reproduction of the spinifex hopping mouse (*Notomys alexis*) in the natural environment. *Australian Journal of Zoology* **40**, 57–71.
- BROWN, J. H. & ZENG, Z. (1989). Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. *Ecology* **70**, 1507–1525.
- BRUNO, J. F., STACHOWICZ, J. J. & BERTNESS, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**, 119–125.
- BURBIDGE, A. A., JOHNSON, K. A., FULLER, P. J. & SOUTHGATE, R. I. (1988). Aboriginal knowledge of the mammals of the central deserts of Australia. *Australian Wildlife Research* **15**, 9–39.
- BURBIDGE, A. A. & MCKENZIE, N. L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**, 143–198.
- BURROWS, N. D. & CHRISTENSEN, P. E. S. (1990). A survey of Aboriginal fire patterns in the western desert of Australia. In: *Fire and the environment: ecological and cultural perspectives*. (eds S. C. NODVIN & T. A. WALDORP), pp. 297–305. U.S. Department of Agriculture, Southeastern Forest Experimental Station, Asheville, North Carolina.
- CARSTAIRS, J. L. (1976). Population dynamics and movements of *Rattus villosissimus* (Waite) during the 1966–69 plague at Brunette Downs, NT. *Australian Wildlife Research* **3**, 1–9.
- CATENAZZI, A. & DONNELLY, M. A. (2007). The *Ulva* connection: marine algae subsidize terrestrial predators in coastal Peru. *Oikos* **116**, 75–86.
- CAUGHLEY, G. (1994). Directions in conservation biology. *Journal of Animal Ecology* **63**, 215–244.
- CAUGHLEY, G., GRIGG, G. C., CAUGHLEY, J. & HILL, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* **7**, 1–12.
- CAUGHLEY, G. & SINCLAIR, A. R. E. (1994). *Wildlife ecology and management*. Blackwell Scientific Publications, Oxford.

- CHAN, K. (2001). Partial migration in Australian landbirds: a review. *Emu* **101**, 281–292.
- CHEN, X., DICKMAN, C. R. & THOMPSON, M. B. (1998). Diet of the mulgara, *Dasyurus cristicauda* (Marsupialia: Dasyuridae), in the Simpson Desert, central Australia. *Wildlife Research* **25**, 233–242.
- CHIEW, F. H. S., PIECHOTA, T. C., DRACUP, J. A. & MCMAHON, T. A. (1998). El Niño/Southern Oscillation and Australian rainfall, streamflow and drought: links and potential for forecasting. *Journal of Hydrology* **204**, 138–149.
- CHOQUENOT, D., MCILROY, J. & KORN, T. (1996). *Managing vertebrate pests: feral pigs*. Bureau of Resource Sciences, Australian Government Publishing Service, Canberra.
- CLELAND, J. B. (1918). Previous phenomenal visitations of rats or mice in Australia. *Journal and Proceedings of the Royal Society of New South Wales* **52**, 123–165.
- CLOUDSLEY-THOMPSON, J. L. (1991). *Ecophysiology of desert arthropods and reptiles*. Springer-Verlag, Berlin.
- CONNELL, J. H. & SOUSA, W. P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist* **121**, 789–824.
- CORBETT, L. K. & NEWSOME, A. E. (1987). The feeding ecology of the dingo III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternating predation. *Oecologia* **74**, 215–227.
- COVENTRY, A. J. & DIXON, J. M. (1984). Small native mammals from the Chinaman Well area, north-western Victoria. *Australian Mammalogy* **7**, 111–115.
- CROMBIE, A. C. (1944). Rat plagues in western Queensland. *Nature* **154**, 803–804.
- DAVIES, S. (1984). Nomadism as a response to desert conditions in Australia. *Journal of Arid Environments* **7**, 183–195.
- DEGEN, A. A. (1997). *Ecophysiology of small desert mammals*. Springer, Berlin.
- DENNY, M. J. S. (1982). Adaptations of the red kangaroo and euro (Macropodidae) to aridity. In: *Evolution of the flora and fauna of arid Australia*. (eds W. R. BARKER & P. J. M. GREENSLADE), pp. 179–183. Peacock Publications, Adelaide.
- DIAZ, H. F. & MARKGRAF, V. (1992). *El Niño: historical and paleoclimatic aspects of the southern oscillation*. Cambridge University Press, Cambridge.
- DICKMAN, C. R. (1996a). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**, 185–195.
- DICKMAN, C. R. (1996b). Incorporating science into recovery planning for threatened species. In: *Back from the brink: refining the threatened species recovery process*. (eds S. STEPHENS & S. MAXWELL), pp. 63–73. Surrey Beatty & Sons, Sydney.
- DICKMAN, C. R. (2006). Species interactions: indirect effects. In: *Ecology: an Australian perspective*, 2nd edition. (eds P. ATTIWILL & B. A. WILSON), pp. 303–316. Oxford University Press, Oxford.
- DICKMAN, C. R., DOWNEY, F. J. & PREDAVEC, M. (1993a). The hairy-footed dunnart *Sminthopsis hirtipes* (Marsupialia: Dasyuridae) in Queensland. *Australian Mammalogy* **16**, 69–72.
- DICKMAN, C. R., HAYTHORNTHWAITE, A. S., MCNAUGHT, G. H., MAHON, P. S., TAMAYO, B. & LETNIC, M. (2001). Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research* **28**, 493–506.
- DICKMAN, C. R., HENRY-HALL, N. J., LLOYD, H. & ROMANOW, K. A. (1991). A survey of the terrestrial vertebrate fauna of Mount Walton, western Goldfields, Western Australia. *Western Australian Naturalist* **18**, 200–206.
- DICKMAN, C. R., LETNIC, M. & MAHON, P. S. (1999a). Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall. *Oecologia* **119**, 357–366.
- DICKMAN, C. R., LUNNEY, D. & BURGIN, S. (eds) (2007). *Animals of arid Australia: out on their own?* Royal Zoological Society of New South Wales, Sydney.
- DICKMAN, C. R., MAHON, P. S., MASTERS, P. & GIBSON, D. F. (1999b). Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research* **26**, 389–403.
- DICKMAN, C. R., PREDAVEC, M. & DOWNEY, F. J. (1995). Long-range movements of small mammals in arid Australia: implications for land management. *Journal of Arid Environments* **31**, 441–452.
- DICKMAN, C. R., PRESSEY, R. L., LIM, L. & PARNABY, H. E. (1993b). Mammals of particular conservation concern in the Western Division of New South Wales. *Biological Conservation* **65**, 219–248.
- DICKMAN, C. R. & READ, D. G. (1992). The biology and management of dasyurids of the arid zone in New South Wales. *New South Wales National Parks and Wildlife Service Species Management Report* **11**, 1–112.
- DUBLIN, H. T., SINCLAIR, A. R. E. & MCGLADE, J. (1990). Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**, 1147–1164.
- DUNCAN, F. D. & DICKMAN, C. R. (2001). Respiratory patterns and metabolism in tenebrionid and carabid beetles from the Simpson Desert, Australia. *Oecologia* **129**, 509–517.
- DUNLOP, J. N. & SAWLE, M. (1980). The small mammals of the eastern Pilbara and Hamersley Range National Park. In: *A fauna survey of the Hamersley Range National Park*. (ed. B. G. MUIR), pp. 26–30. National Parks Authority of Western Australia, Perth.
- DU PLESSIS, W. P. (1999). Linear regression relationships between NDVI, vegetation and rainfall in Etosha National Park, Namibia. *Journal of Arid Environments* **42**, 235–260.
- EASTERLING, D. R., MEEHL, G. A., PARMESAN, C., CHANGNON, S. A., KARL, T. R. & MEARN, L. O. (2000). Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074.
- ECCARD, J. A., WATHER, A. R. B. & MILTON, S. J. (2000). How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments* **46**, 103–106.
- EVENARI, M., NOY-MEIR, I. & GOODALL, D. W., eds. (1985). *Hot deserts and arid shrublands*. Elsevier, Amsterdam.
- FINLAYSON, H. H. (1939a). On mammals from the Lake Eyre Basin. Part IV. The Monodelphia. *Transactions of the Royal Society of South Australia* **63**, 88–117.
- FINLAYSON, H. H. (1939b). On mammals from the Lake Eyre Basin. Part V. General remarks on the increase of murids and their population movements in the Lake Eyre Basin during the years 1930–1936. *Transactions of the Royal Society of South Australia* **63**, 348–353.
- FINLAYSON, H. H. (1941). On central Australian mammals. Part II. The Muridae. *Transactions of the Royal Society of South Australia* **65**, 215–231.
- FLANNERY, T. F. (1994). *The future eaters: an ecological history of the Australasian lands and people*. Reed Books, Sydney.
- FOX, B. J. (1982). Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* **63**, 1332–1341.
- FRANK, A. S. K., DICKMAN, C. R. & WARDLE, G. M. (2008). Responses of small mammals and lizards to cattle grazing and cattle removal in arid Australia. In: *Proceedings of the Australian*

- Rangeland Society Conference*, Charters Towers, pp. 7–10. Australian Rangeland Society, Brisbane, Australia.
- FRANK, A. & SODERQUIST, T. (2005). The importance of refuge habitat in the local conservation of stripe-faced dunnarts *Sminthopsis macroura* on arid rangelands. *Australian Mammalogy* **27**, 75–79.
- FRIEND, G. R., JOHNSON, B. W., MITCHELL, D. S. & SMITH, G. T. (1997). Breeding, population dynamics and habitat relationships of *Sminthopsis dolichura* (Marsupialia: Dasyuridae) in semi-arid shrublands of Western Australia. *Wildlife Research* **24**, 245–262.
- GEISER, F. (2004). The role of torpor in the life of Australian arid zone mammals. *Australian Mammalogy* **26**, 125–134.
- GILFILLAN, S. L. (2001). An ecological study of a population of *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae) in central Australia. I. Invertebrate food supply, diet and reproductive strategy. *Wildlife Research* **28**, 469–480.
- GREENVILLE, A. C., DICKMAN, C. R., WARDLE, G. M. & LETNIC, M. (2009). The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* **18**, 631–639.
- GRIFFIN, G. F. (1984). Hummock grasslands. In: *Management of Australia's rangelands*. (eds G. N. HARRINGTON, A. D. WILSON & M. D. YOUNG), pp. 271–284. CSIRO Publishing, Melbourne.
- GROSBOIS, V., GIMENEZ, O., GAILLARD, J.-M., PRADEL, R., BARBRAUD, C., CLOBERT, J., MØLLER, A. P. & WEIMERSKIRCH, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* **83**, 357–399.
- HAPPOLD, M. (1976). Reproductive biology and development in the conilurine rodents (Muridae) of Australia. *Australian Journal of Zoology* **24**, 19–26.
- HARRINGTON, G. N., WILSON, A. D. & YOUNG, M. D., eds. (1984). *Management of Australia's rangelands*. CSIRO Publishing, Melbourne.
- HARRISON, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**, 73–88.
- HAYDON, D. T., FRIAR, J. K. & PIANKA, E. R. (2000). Fire-driven dynamic mosaics in the Great Victoria Desert, Australia—I. Fire geometry. *Landscape Ecology* **15**, 373–382.
- HAYTHORNTHWAITE, A. S. & DICKMAN, C. R. (2000). Foraging strategies of an insectivorous marsupial, *Sminthopsis youngsoni* (Marsupialia: Dasyuridae), in Australian sandridge desert. *Austral Ecology* **25**, 193–198.
- HAYTHORNTHWAITE, A. S. & DICKMAN, C. R. (2006a). Distribution, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. *Ecography* **29**, 285–300.
- HAYTHORNTHWAITE, A. S. & DICKMAN, C. R. (2006b). Long-distance movements by a small carnivorous marsupial: how *Sminthopsis youngsoni* (Marsupialia: Dasyuridae) uses habitat in an Australian sandridge desert. *Journal of Zoology* **270**, 543–549.
- HAYWARD, B., HESKE, E. J. & PAINTER, C. W. (1997). Effects of livestock grazing on small mammals at a desert cienega. *Journal of Wildlife Management* **61**, 123–129.
- HJELLE, B. & GLASS, G. E. (2000). Outbreak of hantavirus infection in the Four Corners region of the United States in the wake of the 1997–1998 El Niño–Southern Oscillation. *Journal of Infectious Disease* **181**, 1569–1573.
- HOLDEN, C. & MUTZE, G. (2002). Impact of rabbit haemorrhagic disease on introduced predators in the Flinders Ranges, South Australia. *Wildlife Research* **29**, 615–626.
- HOLM, A. M. R. & ALLEN, R. J. (1988). Seasonal changes in the nutritive value of grass species in spinifex pastures of Western Australia. *Australian Rangeland Journal* **10**, 60–64.
- HOLMGREN, M., STAPP, P., DICKMAN, C. R., GRACIA, C., GRAHAM, S., GUTIÉRREZ, J. R., HICE, C., JAKSIC, F., KELT, D. A., LETNIC, M., LIMA, M., LÓPEZ, B. C., MESERVE, P. L., MILSTEAD, W. B., POLIS, G. A., PREVITALI, M. A., RICHTER, M., SABATÉ, S. & SQUEO, F. A. (2006a). A synthesis of ENSO effects on drylands in Australia, North America and South America. *Advances in Geosciences* **6**, 69–72.
- HOLMGREN, M., STAPP, P., DICKMAN, C. R., GRACIA, C., GRAHAM, S., GUTIÉRREZ, J. R., HICE, C., JAKSIC, F., KELT, D. A., LETNIC, M., LIMA, M., LÓPEZ, B. C., MESERVE, P. L., MILSTEAD, W. B., POLIS, G. A., PREVITALI, M. A., RICHTER, M., SABATÉ, S. & SQUEO, F. A. (2006b). Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment* **4**, 87–95.
- HOW, R. A. & COOPER, N. K. (2002). Terrestrial small mammals of the Abydos Plain in the north-eastern Pilbara, Western Australia. *Journal of the Royal Society of Western Australia* **85**, 71–82.
- HUGHES, L. (2003). Climate change and Australia: Trends projections and impacts. *Austral Ecology* **28**, 423–443.
- HUNTER, D. M. & MELVILLE, M. D. (1994). The rapid and long-lasting growth of grasses following small falls of rain on stony downs in the arid interior of Australia. *Austral Ecology* **19**, 46–51.
- HUXMAN, T. E., SNYDER, K. A., TISSUE, D., LEFFLER, A. J., OGLE, K., POCKMAN, W. T., SANDQUIST, D. R., POTTS, D. L. & SCHWINNING, S. (2004). Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* **141**, 254–268.
- IDRIS, M. (2005). Significance of scent marking gland in desert rodents. In: *Changing faunal ecology in the Thar Desert*. (eds B. K. TYAGI & Q. H. BAQRI), pp. 267–288. Scientific Publishers, Jodhpur.
- JAKSIC, F. M. & LIMA, M. (2003). Myths and facts on ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecology* **28**, 237–251.
- JAKSIC, F. M., SILVA, S. I., MESERVE, P. L., & GUTIÉRREZ, J. R. (1997). A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos* **78**, 341–354.
- JAMES, C. D., LANDSBERG, J. & MORTON, S. R. (1995). Ecological functioning in arid Australia and research to assist conservation of biodiversity. *Pacific Conservation Biology* **2**, 126–142.
- KELLY, D. & SORK, V. L. (2002). Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**, 427–447.
- KINGSFORD, R. T., CURTIN, A. L. & PORTER, J. (1999a). Water flows on Cooper Creek in arid Australia determine 'boom' and 'bust' periods for waterbirds. *Biological Conservation* **88**, 231–248.
- KINGSFORD, R. T., WONG, P. S., BRAITHWAITE, L. W. & MAHER, M. T. (1999b). Waterbird abundance in eastern Australia, 1983–92. *Wildlife Research* **26**, 351–366.
- KINNEAR, J. E., SUMNER, N. R. & ONUS, M. L. (2002). The red fox in Australia – an exotic predator turned biocontrol agent. *Biological Conservation* **108**, 335–359.
- KOENIG, W. D. & KNOPS, J. M. H. (2000). Patterns of annual seed production by Northern Hemisphere trees: a global perspective. *American Naturalist* **155**, 59–69.
- KÖRTNER, G., PAVEY, C. R. & GEISER, F. (2007). Spatial ecology of the mulgara in arid Australia: impact of fire history on home range size and burrow use. *Journal of Zoology* **273**, 350–357.
- KOTLER, B. P., BROWN, J. S. & MITCHELL, W. A. (1994). The role of predation in shaping the behaviour, morphology and

- community organisation of desert rodents. *Australian Journal of Zoology* **42**, 449–466.
- KOTLER, B. P., DICKMAN, C. R. & BROWN, J. S. (1998). The effects of water on patch use by two Simpson Desert granivores (*Corvus coronoides* and *Pseudomys hermannsburgensis*). *Australian Journal of Ecology* **23**, 574–578.
- KOTWICKI, V. & ALLAN, R. (1998). La Niña de Australia-contemporary and palaeo-hydrology of Lake Eyre. *Palaeogeography, Palaeoclimatology, Palaeoecology* **144**, 265–280.
- KUTT, A. S., THURGATE, N. Y. & HANNAH, D. S. (2004). Distribution and habitat of the desert mouse (*Pseudomys desertor*) in Queensland. *Wildlife Research* **31**, 129–142.
- LANGLANDS, P. R., BRENNAN, K. E. C. & PEARSON, D. J. (2006). Spiders, spinifex, rainfall and fire: long-term changes in an arid spider assemblage. *Journal of Arid Environments* **67**, 36–59.
- LAW, B. S. & DICKMAN, C. R. (1998). The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity and Conservation* **7**, 323–333.
- LETNIC, M. (2002). Long distance movements and the use of fire mosaics by small mammals in the Simpson Desert, central Australia. *Australian Mammalogy* **23**, 125–134.
- LETNIC, M. (2003). The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. *Wildlife Research* **30**, 547–563.
- LETNIC, M. (2004). Cattle grazing in a hummock grassland regenerating after fire: the short-term effects of cattle exclusion on vegetation in south-western Queensland. *Rangeland Journal* **26**, 34–48.
- LETNIC, M. (2007). The impacts of pastoralism on the fauna of arid Australia. In: *Animals of arid Australia: out on their own?* (eds C. R. DICKMAN, D. LUNNEY & S. BURGIN), pp. 65–75. Royal Zoological Society of New South Wales, Sydney.
- LETNIC, M., CROWTHER, M. S. & KOCH, F. (2009a). Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* **12**, 302–312.
- LETNIC, M. & DICKMAN, C. R. (2005). The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology* **30**, 24–39.
- LETNIC, M. & DICKMAN, C. R. (2006). Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation* **15**, 3847–3880.
- LETNIC, M., DICKMAN, C. R., TISCHLER, M. K., TAMAYO, B. & BEH, C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments* **59**, 85–114.
- LETNIC, M. & KOCH, F. (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology*, in press.
- LETNIC, M., KOCH, F., GORDON, C., CROWTHER, M. S. & DICKMAN, C. R. (2009b). Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society (London)-Biology* **276**, 3249–3256.
- LETNIC, M., TAMAYO, B. & DICKMAN, C. R. (2005). The responses of mammals to La Niña (El Niño Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**, 689–703.
- LEWIS, T. L., MEWS, M., JELINSKI, D. E. & ZIMMER, M. (2007). Detrital subsidy to the supratidal zone provides feeding habitat for intertidal crabs. *Estuaries and Coasts* **30**, 451–458.
- LI, H. & ZHANG, Z. (2007). Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management* **242**, 511–517.
- LIM, L. (1992). *Recovery plan for the kowari *Dasyuroides byrnei* Spencer, 1896 (Marsupialia: Dasyuridae)*. Australian National Parks and Wildlife Service, Canberra.
- LOW, B. S. (1979). The predictability of rain and the foraging patterns of the red kangaroo (*Megaleia rufa*) in central Australia. *Journal of Arid Environments* **2**, 61–72.
- LUDWIG, J., TONGWAY, D., FREUDENBERGER, D., NOBLE, J. & HODGKINSON, K., eds. (1997). *Landscape ecology: function and management. Principles from Australia's rangelands*. CSIRO Publishing, Melbourne.
- LUNDIE-JENKINS, G. (1993). Ecology of the rufous hare-wallaby, *Lagorchestes hirsutus* Gould (Marsupialia: Macropodidae), in the Tanami Desert, Northern Territory. I. Patterns of habitat use. *Wildlife Research* **20**, 457–476.
- LUNNEY, D. (2001). Causes of the extinction of native mammals of the Western Division of New South Wales: an ecological interpretation of the nineteenth century historical record. *Rangeland Journal* **23**, 44–70.
- MACK, A. (1961). Mammals from south-western Queensland. *Memoirs of the Queensland Museum* **13**, 213–228.
- MAHON, P. S. (1999). Predation by feral cats and red foxes, and the dynamics of small mammal populations in arid Australia. PhD thesis, University of Sydney, Sydney.
- MARTIN, G. (2003). The role of small ground-foraging mammals in topsoil health and biodiversity: implications for management and restoration. *Ecological Management and Restoration* **4**, 114–118.
- MASTERS, P. (1993). The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**, 803–813.
- MASTERS, P. (1996). The effects of fire-driven succession on reptiles in spinifex grasslands at Uluru National Park, Northern Territory. *Wildlife Research* **23**, 39–48.
- MASTERS, P. (1998). The mulgara *Dasyercus cristicauda* (Marsupialia: Dasyuridae) at Uluru National Park, Northern Territory. *Australian Mammalogy* **20**, 403–407.
- MASTERS, P., DICKMAN, C. R. & CROWTHER, M. S. (2003). Effects of cover reduction on mulgara *Dasyercus cristicauda* (Marsupialia: Dasyuridae), rodent and invertebrate populations in central Australia: implications for land management. *Austral Ecology* **28**, 658–665.
- MAY, R. M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**, 471–477.
- MCCARTHY, M. A. (1996). Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* **33**, 45–53.
- McFARLAND, D. (1992). *Fauna of the Channel Country biogeographic region, south west Queensland*. Queensland National Parks and Wildlife Service, Brisbane.
- MCKENZIE, N. L., BURBIDGE, A. A., BAYNES, A., BRERETON, R. N., DICKMAN, C. R., GORDON, G., GIBSON, L. A., MENKHORST, P. W., ROBINSON, A. C., WILLIAMS, M. R. & WOJNARSKI, J. C. Z. (2007). Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34**, 597–611.
- MCRAE, P. D. (2004). Aspects of the ecology of the greater bilby, *Macrotis lagotis*, in Queensland. MSc thesis, University of Sydney, Sydney.
- MESERVE, P. L., GUTIÉRREZ, J. R., YUNGER, J. A., CONTRERAS, L. C. & JAKSIC, F. M. (1996). Role of biotic interactions in a small mammal assemblage in semiarid Chile. *Ecology* **77**, 133–148.

- MESERVE, P. L., KELT, D. A., MILSTEAD, W. B. & GUTIÉRREZ, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *BioScience* **53**, 633–646.
- MESERVE, P. L., YUNGER, J. A., GUTIÉRREZ, J. R., CONTRERAS, L. C., MILSTEAD, W. B., LANG, B. K., CRAMER, K. L., HERRERA, S., LAGOS, V. O., SILVA, S. I., TABILO, E. L., TORREALBA, M.-A. & JAKSIC, F. M. (1995). Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. *Journal of Mammalogy* **76**, 580–595.
- MORTON, S. R. (1978a). An ecological study of *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae). II. Behaviour and social organization. *Australian Wildlife Research* **5**, 163–182.
- MORTON, S. R. (1978b). Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *Journal of Mammalogy* **59**, 569–575.
- MORTON, S. R. (1982). Dasyurid marsupials of the Australian arid zone: an ecological review. In: *Carnivorous marsupials*. (ed. M. ARCHER), pp. 117–130. Royal Zoological Society of New South Wales, Sydney.
- MORTON, S. R. (1990). The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**, 201–213.
- MORTON, S. R. & BAYNES, A. (1985). Small mammal assemblages in arid Australia: a reappraisal. *Australian Mammalogy* **8**, 159–169.
- MORTON, S. R., BROWN, J. H., KELT, D. A. & REID, J. A. (1994). Comparison of community structure of small mammals of north American and Australian deserts. *Australian Journal of Zoology* **42**, 501–525.
- MORTON, S. R., DICKMAN, C. R. & FLETCHER, T. P. (1989). Dasyuridae. In: *Fauna of Australia*, volume 1B, *Mammalia*. (eds D. W. WALTON & B. J. RICHARDSON), pp. 560–582. Australian Government Publishing Service, Canberra.
- MORTON, S. R., HAPPOLD, M., LEE, A. K. & MACMILLEN, R. E. (1977). The diet of the barn owl, *Tyto alba*, in south-western Queensland. *Australian Wildlife Research* **4**, 91–97.
- MORTON, S. R. & MARTIN, A. A. (1979). Feeding ecology of the barn owl, *Tyto alba*, in arid southern Australia. *Australian Wildlife Research* **6**, 191–204.
- MORTON, S. R., SHORT, J. & BARKER, R. D. (1995). *Refugia for biological diversity in arid and semi-arid Australia*. Department of the Environment, Sport and Territories, Canberra.
- MOSEBY, K. E. & READ, J. L. (1999). Population dynamics and movement patterns of Bolam's mouse, *Pseudomys bolami*, at Roxby Downs, South Australia. *Australian Mammalogy* **20**, 353–368.
- MOSEBY, K. E., OWENS, H., BRANDLE, R., BICE, J. K. & GATES, J. (2006). Variation in population dynamics and movement patterns between two geographically isolated populations of the dusky hopping mouse (*Notomys fuscus*). *Wildlife Research* **33**, 223–232.
- MOSEBY, K. E., HILL, B. M. & READ, J. L. (2009). Arid recovery—A comparison of reptile and small mammal populations inside and outside a large cat and fox-proof enclosure in arid South Australia. *Austral Ecology* **34**, 156–169.
- MURRAY, B. R. & DICKMAN, C. R. (1994). Granivory and microhabitat use in Australian desert rodents: are seeds important? *Oecologia* **99**, 216–225.
- MURÚA, R., GONZÁLEZ, L. A. & LIMA, M. (2003). Population dynamics of rice rats (a hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations. *Oikos* **102**, 137–145.
- MYERS, K. & PARKER, B. S. (1975a). A study of the biology of the wild rabbit in climatically different regions in eastern Australia. VI. Changes in numbers and distribution related to climate and land systems in semiarid north-western New South Wales. *Australian Wildlife Research* **2**, 11–32.
- MYERS, K. & PARKER, B. S. (1975b). Effect of severe drought on rabbit numbers and distribution in a refuge area in semiarid north-western New South Wales. *Australian Wildlife Research* **2**, 103–120.
- NEWSOME, A. E. (1965). The abundance of red kangaroos, *Megaleia rufa* (Desmarest), in central Australia. *Australian Journal of Zoology* **13**, 735–759.
- NEWSOME, A. E. (1971). The ecology of red kangaroos. *Australian Zoologist* **16**, 32–50.
- NEWSOME, A. E., CATLING, P. C., COOKE, B. D. & SMYTH, R. (2001). Two ecological universes separated by the dingo barrier fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* **23**, 71–98.
- NEWSOME, A. E. & CORBETT, L. K. (1975). Outbreaks of rodents in semi-arid and arid Australia: causes, preventions, and evolutionary considerations. In: *Rodents in desert environments*. (eds I. PRAKASH & P. K. GHOSH), pp. 117–153. Dr W. Junk, The Hague.
- NEWSOME, A. E., PARER, I. & CATLING, P. C. (1989). Prolonged prey suppression by carnivores – predator-removal experiments. *Oecologia* **78**, 458–467.
- NICHOLLS, N. (1991). The El Niño/Southern Oscillation and Australian vegetation. *Plant Ecology* **91**, 23–36.
- NOBLE, J. C. (1989). Fire studies in mallee (*Eucalyptus* spp.) communities of western New South Wales: the effects of fires applied in different seasons on herbage productivity and their implications for management. *Australian Journal of Ecology* **14**, 169–187.
- NOY-MEIR, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**, 25–51.
- NOY-MEIR, I. (1975). Stability of grazing systems: an application of predator-prey graphs. *Journal of Ecology* **63**, 459–481.
- ORIAN, G. H. & MILEWSKI, A. V. (2007). Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82**, 393–423.
- OSTFELD, R. S., JONES, C. G. & WOLFF, J. O. (1996). Of mice and mast: ecological connections in eastern deciduous forests. *BioScience* **46**, 323–330.
- OSTFELD, R. S. & KEESING, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* **15**, 232–237.
- OSTFELD, R. S. & KEESING, F. (2007). Pulsed resources and community responses: an exploration of factors influencing outcomes. In: *Temporal dimensions of landscape ecology: wildlife responses to variable resources*. (eds J. A. BISSONNETTE & I. STORCH), pp. 30–42. Springer, New York.
- PALTRIDGE, R. (2002). The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**, 389–403.
- PALTRIDGE, R. & SOUTHGATE, R. (2001). The effect of habitat type and seasonal conditions on fauna in two areas of the Tanami Desert. *Wildlife Research* **28**, 247–260.
- PARER, I. (1977). The population ecology of the wild rabbit *Oryctolagus cuniculus* (L.) in a Mediterranean-type climate in New South Wales. *Australian Wildlife Research* **4**, 171–205.
- PAVEY, C. R., ELDRIDGE, S. R. & HEYWOOD, M. (2008). Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy* **89**, 674–683.

- PAVEY, C. R., GOODSHIP, N. & GEISER, F. (2003). Home range and spatial organisation of rock-dwelling carnivorous marsupial, *Pseudantechinus macdonnellensis*. *Wildlife Research* **30**, 135–142.
- PETRAITIS, P. S. & LATHAM, R. E. (1999). The importance of scale in testing the origins of alternative community states. *Ecology* **80**, 429–442.
- PETTIGREW, J. D. (1993). A burst of feral cats in the Diamantina: a lesson for the management of pest species? In: *Cat management workshop proceedings*. (eds G. SIEPEN & C. OWENS), pp. 25–32. Queensland Department of Environment and Heritage, Brisbane.
- PIANKA, E. R. (1986). *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press, New Jersey.
- PIANKA, E. R. (1996). Long-term changes in lizard assemblages in the Great Victoria Desert: dynamic habitat mosaics in response to wildfires. In: *Long-term studies of vertebrate communities*. (eds M. L. CODY & J. A. SMALLWOOD), pp. 191–213. Academic Press, New York.
- PLOMLEY, N. J. B. (1972). Some notes on plagues of small mammals in Australia. *Journal of Natural History* **6**, 363–384.
- POPLE, A. R., GRIGG, G. C., CAIRNS, S. C., ALEXANDER, P., BEARD, L. A. & HENZELL, R. P. (1996). Trends in numbers and changes in the distribution of feral goats (*Capra hircus*) in the South Australian pastoral zone. *Wildlife Research* **23**, 687–696.
- POPLE, A. R., GRIGG, G. C., CAIRNS, S. C., BEARD, L. A. & ALEXANDER, P. (2000). Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**, 269–276.
- PREDAVEC, M. (1994a). Food limitation and demography in Australian desert rodents. PhD thesis, University of Sydney, Sydney.
- PREDAVEC, M. (1994b). Population dynamics and environmental changes during natural eruptions of Australian desert rodents. *Wildlife Research* **21**, 569–582.
- PREDAVEC, M. (2000). Food limitation in Australian desert rodents: experiments using supplementary feeding. *Oikos* **91**, 512–522.
- PREDAVEC, M. & DICKMAN, C. R. (1994). Population dynamics and habitat use of the long-haired rat (*Rattus villosissimus*) in south-western Queensland. *Wildlife Research* **21**, 1–10.
- READ, D. G. (1984a). Diet and habitat preference of *Leggadina forresti* (Rodentia: Muridae) in western New South Wales. *Australian Mammalogy* **7**, 215–217.
- READ, D. G. (1984b). Movements and home ranges of three sympatric dasyurids, *Sminthopsis crassicaudata*, *Planigale gilesi* and *P. tenuirostris* (Marsupialia), in semiarid western New South Wales. *Australian Wildlife Research* **11**, 223–234.
- READ, D. G. (1984c). Reproduction and breeding season of *Planigale gilesi* and *P. tenuirostris* (Marsupialia: Dasyuridae). *Australian Mammalogy* **7**, 161–173.
- READ, J. L. (1992). Influence of habitats, climate, grazing and mining on terrestrial vertebrates at Olympic Dam, South Australia. *The Rangeland Journal* **14**, 143–156.
- READ, J. L. (1997). Stranded on desert islands? Factors shaping animal populations in Lake Eyre South. *Global Ecology and Biogeography Letters* **6**, 431–438.
- READ, J. L. (2002). Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. *Austral Ecology* **27**, 55–66.
- READ, J. & BOWEN, Z. (2001). Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* **28**, 195–203.
- READ, J. L. & WILSON, D. (2004). Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. *Wildlife Research* **31**, 51–56.
- READ, J. L., COPLEY, P. & BIRD, P. (1999). The distribution, ecology and current status of *Pseudomys desertor* in South Australia. *Wildlife Research* **28**, 195–203.
- RISBEY, D. A., CALVER, M. C., SHORT, J., BRADLEY, J. S. & WRIGHT, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* **27**, 223–235.
- ROBINSON, A. C., KEMPER, C. M., MEDLIN, G. C. & WATTS, C. H. S. (2000). The rodents of South Australia. *Wildlife Research* **27**, 379–404.
- ROBINSON, A. C., LIM, L., CANTY, P. D., JENKINS, R. B. & MACDONALD, C. A. (1994). Studies of the yellow-footed rock-wallaby, *Petrogale xanthopus* Gray (Marsupialia: Macropodidae). Population studies at Middle Gorge, South Australia. *Wildlife Research* **21**, 473–481.
- ROBINSON, M. D. (1990). Comments on the reproductive biology of the Namib Desert dune lizard, *Aporosaurus anchietae*, during two years of very different rainfall. In: *Namib ecology: 25 years of Namib research*. (ed. M. K. SEELY), pp. 163–168. Transvaal Museum, Pretoria.
- SALO, P., KORPIMÄKI, E., BANKS, P. B., NORDSTRÖM, M. & DICKMAN, C. R. (2007). Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society of London*, **B 274**, 1237–1243.
- SAUNDERS, G. R. & GILES, J. R. (1977). A relationship between plagues of the house mouse, *Mus musculus* (Rodentia: Muridae) and prolonged periods of dry weather in south-eastern Australia. *Australian Wildlife Research* **4**, 241–247.
- SHAPIRA, I., SULTAN, H. & SHANAS, U. (2008). Agricultural farming alters predator-prey interactions in nearby natural habitats. *Animal Conservation* **11**, 1–8.
- SHARP, A. & NORTON, M. (2000). Dynamics of the New South Wales yellow-footed rock-wallaby population, in relation to rainfall patterns. *Australian Mammalogy* **22**, 71–79.
- SHORT, J. & TURNER, B. (1994). A test of the vegetation mosaic hypothesis: a hypothesis to explain the decline and extinction of Australian mammals. *Conservation Biology* **8**, 439–449.
- SHORT, J. & TURNER, B. (1999). Ecology of burrowing bettongs, *Bettongia lesueur* (Marsupialia: Potoroidae), on Dorre and Bernier Islands, Western Australia. *Wildlife Research* **26**, 651–669.
- SHORT, J., TURNER, B., MAJORS, C. & LEONE, J. (1997). The fluctuating abundance of endangered mammals on Bernier and Dorre Islands, Western Australia – conservation implications. *Australian Mammalogy* **20**, 53–61.
- SINCLAIR, A. R. E., PECH, R. P., DICKMAN, C. R., HIK, D., MAHON, P. & NEWSOME, A. E. (1998). Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**, 564–575.
- SOUTHGATE, R. & MASTERS, P. (1996). Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research* **23**, 289–303.
- SOUTHGATE, R., PALTRIDGE, R., MASTERS, P. & OSTENDORF, B. (2007). Modelling introduced predator and herbivore distributions in the Tanami Desert, Australia. *Journal of Arid Environments* **68**, 438–464.
- STAFFORD SMITH, D. M. & MORTON, S. R. (1990). A framework for the ecology of arid Australia. *Journal of Arid Environments* **18**, 255–278.

- STRONG, B. W. & LOW, W. A. (1986). Recent observations and habitat preference of the kultarr, *Antechinomys laniger*, in the Northern Territory. *Northern Territory Naturalist* **9**, 3–7.
- SUIJENDORP, H. (1981). Responses of the hummock grasslands of northwestern Australia to fire. In: *Fire and the Australian biota*. (eds A. M. GILL, R. H. GROVES & I. R. NOBLE), pp. 417–424. Australian Academy of Science, Canberra.
- THIBAULT, K. M. & BROWN, J. H. (2008). Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences USA* **105**, 3410–3415.
- THOMPSON, G. G. & THOMPSON, S. A. (2008). Spatial variability in terrestrial fauna surveys; a case study from the goldfields of Western Australia. *Journal of the Royal Society of Western Australia* **91**, 219–228.
- THOMSON, P. C. (1992). The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. *Wildlife Research* **19**, 531–541.
- VEGA, R., VÁZQUEZ-DOMÍNGUEZ, E., MEJÍA-PUENTE, A. & CUARÓN, A. D. (2007). Unexpected high levels of genetic variability and the population structure of an island endemic rodent (*Oryzomys couesi cozumelae*). *Biological Conservation* **137**, 210–222.
- WATTS, C. H. S. & ASLIN, H. J. (1974). Notes on the small mammals of north-eastern South Australia and south-western Queensland. *Transactions of the Royal Society of South Australia* **98**, 61–69.
- WESTOBY, M. (1979). Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany* **28**, 169–194.
- WESTOBY, M., WALKER, B. & NOY-MEIR, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**, 266–274.
- WHITE, T. C. R. (2002). Outbreaks of house mice in Australia: limitation by a key resource. *Australian Journal of Agricultural Research* **53**, 505–509.
- WHITE, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews* **83**, 227–248.
- WHITFORD, W. G. (2002). *Ecology of desert systems*. Academic Press, San Diego.
- WILSON, G., DEXTER, N., O'BRIEN, P. & BOMFORD, M. (1992). *Pest animals in Australia: a survey of introduced wild mammals*. Bureau of Rural Resources and Kangaroo Press, Canberra.
- WILSON, P. R., PURDIE, R. W. & AHERN, C. R. (1990). Western arid region land use study – Part IV. Technical Bulletin No. 28. Department of Primary Industries, Brisbane.
- WOODALL, P. F. (1983). Distribution and population dynamics of dingoes (*Canis familiaris*) and feral pigs (*Sus scrofa*) in Queensland, 1945–1976. *Journal of Applied Ecology* **20**, 85–95.
- WOOLLEY, P. A. (1984). Reproduction in *Antechinomys laniger* ('spenceri' form) (Marsupialia: Dasyuridae): field and laboratory investigations. *Australian Wildlife Research* **11**, 481–489.
- WOOLLEY, P. A. (1990). Mulgaras, *Dasyercus cristicauda* (Marsupialia: Dasyuridae); their burrows and records of attempts to collect live animals between 1966 and 1979. *Australian Mammalogy* **13**, 61–64.
- WOOLLEY, P. A. (1991). Reproduction in *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae): field and laboratory observations. *Wildlife Research* **18**, 13–25.
- YANG, L. (2004). Periodical cicadas as resource pulses in North American forests. *Science* **306**, 1565–1567.
- YOUNG, M. D. (1979). Influencing land use in pastoral Australia. *Journal of Arid Environments* **2**, 279–288.