

Population dynamics and spatial ecology of a declining desert rodent, *Pseudomys australis*: the importance of refuges for persistence

CHRIS R. PAVEY,* JEFF R. COLE, PETER J. McDONALD, AND CATHERINE E. M. NANO

Biodiversity Unit, Department of Natural Resources, Environment, the Arts and Sport, P.O. Box 1120, Alice Springs, Northern Territory 0871, Australia (CRP, JRC, PJM, CEMN)

CSIRO Ecosystem Sciences, P.O. Box 2111, Alice Springs, Northern Territory 0871, Australia (CRP)

* Correspondent: chris.pavey@csiro.au

Desert rodents exhibit irruptive (boom–bust) population dynamics in response to pulses of primary productivity. Such unpredictable population dynamics are a challenge for monitoring population trends and managing populations, particularly for species in decline. We studied the population dynamics and occurrence of populations of the vulnerable plains mouse, *Pseudomys australis* (42-g body mass), during the low (bust) phase of the cycle in the Simpson Desert, Australia, to examine the use of refuges by the species and the predation pressure experienced from native and introduced predators. Specifically we investigated landscape-scale occurrence; body mass, reproduction, and population size; and presence of native and introduced predators. Our results demonstrate that *P. australis* contracted to discrete areas of the landscape (refuges) during the low phase and that these areas occupied a small proportion (~17%) of the range occupied during population peaks. Animals in refuge populations had comparable body mass, occurred at similar densities to populations during the boom phase, and continued to reproduce during dry conditions. Such refuges represented a significant concentration of biomass to predators in a resource-poor environment. Native predators were rare during the low phase, suggesting that refuges naturally experienced low predation levels. Two introduced predators, feral house cats and red foxes, persisted during the low phase and exploited refuge populations of *P. australis*, thus representing a significant threat to population persistence. We advocate a novel approach to management of rodents in arid systems that involves identifying the discrete parts of the landscape that function as drought refuges and then focusing threat management there. The relatively small size of these refuges increases the likelihood of cost-effective management.

Key words: carnivore, drought, extinction, irruption, population cycle, refuge

© 2014 American Society of Mammalogists

DOI: 10.1644/13-MAMM-A-183

In arid systems, pulses in primary productivity triggered by rare and episodic rainfall events result in extreme fluctuations of rodent populations (Ostfield and Keesing 2000; Previtali et al. 2009), so-called “boom and bust” cycles. During dry (or bust) periods, local extinction and subsequent recolonization by rodent populations have been observed multiple times at long-term monitoring sites across arid regions (e.g., Milstead et al. 2007; Dickman et al. 2011). Currently there is uncertainty over the interpretation of this pattern of occurrence. One interpretation is that irruptive arid rodents persist during the long duration of the low phase at very low population density and that declining detection probabilities make it difficult to monitor them during such periods (e.g., Stapp 2010). However, an alternative explanation is that populations of these species contract to refuge areas or refuge habitats—areas of comparatively high resource availability within the landscape—during

the low phase (Morton 1990; Dickman et al. 2011). For example, in the Norte Chico of north-central Chile, riverine shrublands and fog-forest patches serve as refuges for rodents during dry years within dominant thorn-scrub habitat (Milstead et al. 2007).

Understanding of rodent population dynamics and the role of refuges is a particular challenge in arid Australia for multiple reasons. First, the Australian arid zone is the epicenter of the most dramatic extinction event of native mammals in modern times (Johnson 2006; Burbidge et al. 2008; Woinarski et al. 2011). Simultaneous to the extinction event, most extant terrestrial mammals in arid Australia declined in range and



TABLE 1.—The 4 hypotheses examining occurrence, population dynamics, reproduction, and predation of the plains mouse (*Pseudomys australis*) during the low phase of the population cycle tested during the current study including the predicted outcomes and the variables examined.

Topic	Specific hypothesis	Variables examined and phase of population cycle when assessed
Landscape-scale occurrence	Populations of plains mice persist in refuge sites during the low phase of cycles and occupy a small portion of the range occupied during the boom phase	Occupancy of monitoring sites: low and boom phase Area of occupancy: low and boom phase
Population dynamics and reproduction	Populations contract to refuge sites during the low phase of cycles because these remain areas of high resource availability; therefore, body condition of plains mice in refuge sites is high, population density is high, and reproduction is ongoing	Body mass: low and boom phase Capture rate and number alive at monitoring sites: low phase Proportion subadults: low phase
Native predator occurrence and diet	Native predators are absent or in low abundance during the low phase of cycles; therefore, the level of predation on plains mice by native predators is low	Occurrence and encounter rate of native predators: low phase Diet of native predators: low phase
Introduced predator occurrence and diet	Introduced predators persist in the landscape during the low phase of cycles and exert significant predation pressure on plains mice at refuge sites	Occurrence and encounter rate of cats and foxes: low phase Diet of cats and foxes: low phase

abundance such that they now occupy limited areas of their former ranges (Kinnear et al. 2002). This extinction event in Australia provides an exception to the global trend in which habitat loss and degradation are the key threats to mammal persistence (Cardillo et al. 2006; Wilson et al. 2012). In contrast, there is strong evidence that predation by introduced red foxes (*Vulpes vulpes*) and feral house cats (*Felis catus*) is the dominant causal agent (Burbidge and McKenzie 1989; Quin and Smith 1996; Johnson 2006) and that ongoing predation represents the most significant threat to extant arid-zone mammals (Johnson 2006; McKenzie et al. 2007). Among the mammal groups most severely impacted by predation are the endemic conilurine rodents (Quin and Smith 1996; Burbidge et al. 2008), of which 5 arid-zone species are extinct (3 globally extinct and 2 extinct from mainland Australia) and another 4 are listed as Threatened under Australia's Environment Protection and Biodiversity Conservation Act of 1999.

Second, temporal rainfall variability is not consistent across dryland regions and it is most unpredictable in northern and central Australia and other low-latitude, summer-rainfall regions (van Etten 2009). Such unpredictability is a challenge for managing populations of rodents. Unpredictable population dynamics makes it difficult to know when and where populations will irrupt (Letnic et al. 2011) and, therefore, to design and implement monitoring programs. Further, irruptive rodents remain in the low (bust) phase of the population cycle for the majority of any given time period (Dickman et al. 2010). When populations of these species are declining it is difficult to separate the patterns produced by natural boom–bust cycles from actual population declines, a crucial issue given the importance of effective detection of population trends for the management of threatened species (Joseph et al. 2006).

Given the magnitude of Australia's mammal extinctions and declines on a global scale, the ability of land managers to develop approaches to conserve and (potentially) restore the arid-zone mammal fauna is of international significance. Off-

reserve conservation strategies will need to be a key component of any approach, given that the region follows the national trend of inadequate protection of threatened species within the protected-area system (Watson et al. 2011). Conservation planning for threatened rodents needs to focus on the low phase of cycles when populations are most vulnerable and when small patches of refuge habitat may play a key role in enabling regional persistence (Milstead et al. 2007). Currently limited information is available on the low phase of the population cycle for most arid Australian rodent species.

Here we detail a study designed to examine whether refuges are important sites for the persistence of the plains mouse (*Pseudomys australis*) during the low phase of the population cycle. *P. australis* is a moderate-sized (body mass 42 g) Australian endemic occupying cracking clay and gibber plains in arid central and southern Australia (Brandle et al. 1999). It is classified as Vulnerable nationally, having undergone significant local extinctions since European settlement (Brandle et al. 1999; Brandle and Moseby 1999). The species is nocturnal, sheltering during the day in deep soil cracks or burrows that are typically occupied by a mature female and 1 or 2 generations of offspring. *P. australis* is mostly herbivorous and breeding in the wild is driven by primary productivity following rainfall. The litter size ranges from 1 to 7 with a gestation period of 30–31 days (Brandle and Pavey 2008).

We first examined the pattern of population persistence at a landscape scale to test the hypothesis (Table 1) that populations persist during the low phase in specific areas of the landscape (hereafter referred to as refuges) rather than across the landscape in small, barely detectable, numbers. Second, we hypothesized that refuges contain high-quality habitat and concentrations of resources during dry periods and therefore animals are in good body condition, reproduction occurs, and population density is similar to that in outbreak sites during the boom phase. Third, we examined the pattern of occurrence of and level of predation on *P. australis* by native predators

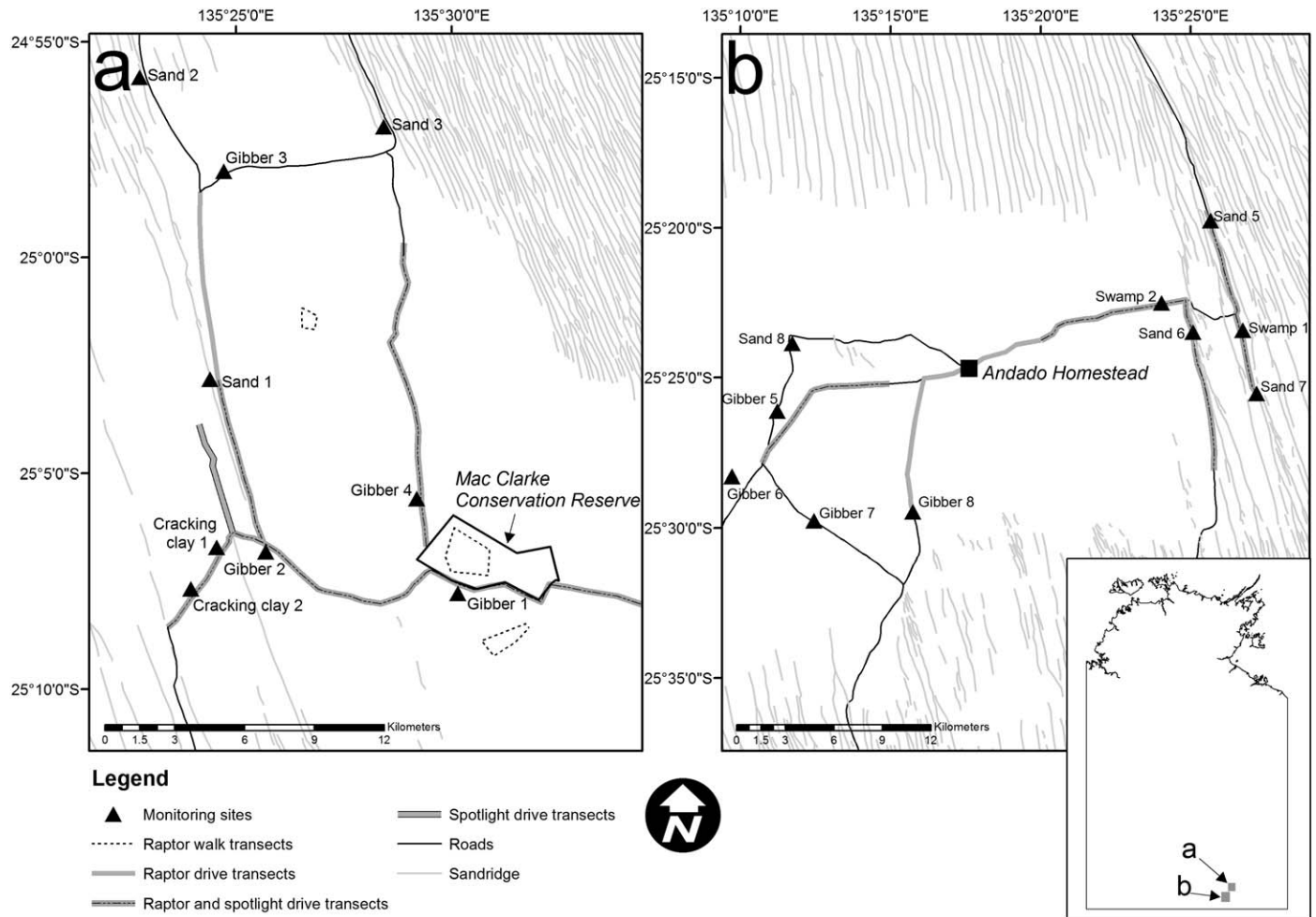


FIG. 1.—Location of study sites during the monitoring #2 study period from October 2007 to May 2011 at Andado Station, Simpson Desert, including small mammal trapping grids, raptor transects, and spotlight transects.

during the low phase, predicting that native predators occur at low densities or are absent during droughts. Therefore, we expected low levels of predation by native predators. Last, we predicted that introduced predators (i.e., red fox and feral house cat) would persist across the landscape during the low phase because of their wide prey range that includes invertebrates, reptiles, birds, and carrion. If the first 2 hypotheses were correct, we predicted that introduced predators would focus foraging on refuges of *P. australis* during the low phase because of the scarcity of food elsewhere across the landscape.

MATERIALS AND METHODS

Study area.—The study area of approximately 7,000 km² is located on Andado Station (25°41'S, 135°29'E; 160 m elevation) in the northwest Simpson Desert, Australia (Fig. 1), a region with irregular and unpredictable rainfall. The average annual rainfall \pm SE at 3 weather stations located within a 50-km radius of the study area is 154.1 \pm 19.0 mm (Australian Bureau of Meteorology climate data online, <http://www.bom.gov.au/climate/data/>, accessed 20 November 2011).

A detailed assessment of rainfall variability in the study area is provided by Nano and Pavey (2013).

Sampling methods.—The study ran from December 1999 to May 2011 and covered 2 boom phases and the intervening low phase. The entire study period was used to assess changes in abundance and area of occupancy by *P. australis*, whereas data collection to test the 4 hypotheses (Table 1) occurred during an intensive fieldwork period from October 2007 to May 2011 (see below for details). This research followed guidelines of the American Society of Mammalogists as detailed in Sikes et al. (2011).

The area of occupancy of *P. australis* was established based on sampling permanent grids using collapsible aluminum box traps (Elliott Scientific Co., Upwey, Victoria, Australia), spotlighting along permanent transects, active searching for the species' distinctive burrows, and carrying out trapping using box traps at one-off survey sites. The occurrence and relative abundance of native and introduced predators was assessed during sampling of permanent spotlight and diurnal transects.

Trapping.—Two monitoring programs were carried out to assess occurrence and abundance of *P. australis*. The 2

programs are hereafter referred to as monitoring #1 and monitoring #2. The sites for monitoring #2 were placed within the areas assessed during monitoring #1 (Fig. 1). The monitoring #1 program was undertaken from 1999 to 2006 on 11 sites, with each site consisting of a line of either 25 or 50 traps spaced 10–15 m apart (see Pavey et al. 2008a for further details). The sites were trapped on 15 occasions during the monitoring #1 program with from 2 to 6 sites being trapped during each monitoring session. The monitoring #2 program was carried out from October 2007 to May 2011 on 20 permanent grids with each grid consisting of 25 box traps set in a 5 × 5 formation with 20 m between adjacent traps. The mean distance between each monitoring site and the next closest site was 4.13 km (± 0.35 SE) with a range of 1.9–7.6 km ($n = 20$).

Trapping grids of monitoring #2 were located in the 5 main habitat types in the study area (Pavey et al. 2011) in proportion to availability: gibber plain (8 sites), cracking clay plain (2), swamp (2), sandridge (7), and sand plain (1). The trap sites were chosen to include habitats where *P. australis* was possibly resident and also areas occupied only during population outbreaks (Brandle et al. 1999).

Eighteen of the monitoring #2 sites were trapped from October 2007 to May 2011, whereas the 2 cracking clay grids were set up in early 2009 and trapped 7 times from March 2009 to May 2011. The average interval of trapping was 3–4 months. Traps were baited with a mixture of peanut butter and rolled oats and left open for 3 or 4 nights per session, giving a total of 15,350 trap-nights (1 trap-night = 1 trap open for 1 night).

In addition to the 2 monitoring programs, trapping was undertaken at 13 additional sites as part of a survey program that sought to locate the species during the low phase within the study area at sites that were not trapped during monitoring. These sites were trapped in May 2008 and May 2009 and each site was trapped on 1 occasion. Trapping was focused on gibber and cracking clay, which are the main habitats of this species (Brandle et al. 1999). Two trapping methods were used. First, 11 sites were trapped using a grid of 25 box traps (set as for the permanent sites, above) that were open for 3 nights. Trap sites were located on gibber plain (5 sites), cracking clay plain (5), and sand plain (1). Traps were baited with a mixture of peanut butter and rolled oats. Second, we established 2 sites on extensive areas of gibber plain that consisted of a long line of box traps (4.8 km and 1.8 km, respectively) set in pairs with adjacent pairs 100 m apart. These lines were open for 3 or 4 nights.

Each animal captured was given a unique number by ear clipping, and weighed to obtain body mass (g). Each animal's reproductive status was assessed as: male—scrotal or nonreproductive, and female—pregnant, lactating, or nonreproductive. Any animal with a body mass < 30 g was classed as subadult (Brandle and Moseby 1999).

Spotlight and diurnal transects.—We used spotlight transects to assess the occurrence of introduced predators, native predators (owls), and of *P. australis*. Although small in size, *P. australis* was readily detected during spotlighting

because of the open nature of the habitat with little vegetation to obscure detection. Nine transects were set up within the study area and either included or were adjacent to each of the trapping grids (Fig. 1). Transects ranged in length from 5.2 to 10.0 km and covered a total of 80.5 km (5.2 km, 6.0 km, 9.3 km, and 6 × 10.0 km). We surveyed each transect during each sampling period except when flooding prevented access. A single observer with a 100-W spotlight sat on the roof of a 4-wheel-drive vehicle moving at 15–20 km/h to detect animals. Surveys commenced approximately 1–2 h after sunset.

We assessed occurrence and relative abundance of diurnal raptors and varanid reptiles using diurnal driving and walking transects. Ten drive transects were set up within the study area and either included or were adjacent to each of the trapping grids (Fig. 1). Transects ranged in length from 5.2 to 23 km and covered a total of 112.5 km (5.2 km, 9.3 km, 6 × 10.0 km, 15.0 km, and 23.0 km). All but 1 of the diurnal drive transects overlapped a nocturnal transect, although 2 were longer than the respective nocturnal transect. We surveyed each transect during each sampling period except when flooding prevented access. Observations were made by an individual sitting in a 4-wheel-drive vehicle moving at 20–30 km/h.

We walked 3 transects, covering a total of 10 km², during each sampling period to search for nesting and roosting raptors. The limited and spatially patchy occurrence of tree cover in the area (see Nano et al. 2012) enabled us to place transects in likely roosting and nesting locations of raptors, especially the main avian predators of *P. australis*: letter-winged kite (*Elanus scriptus*) and barn owl (*Tyto javanica*—Pavey et al. 2008b). Each raptor observed was identified with the use of binoculars.

We used transect data to calculate an index of abundance for each nocturnal species (spotlight transects) and raptors (diurnal transects) expressed as the number of animals observed per kilometer of transect. We applied the methodology in a consistent manner throughout the study and therefore it should accurately reflect changes in abundance across the study period.

Active searching.—Active searching, by vehicle and on foot, was undertaken in cracking clay and gibber habitat to assess the distribution of burrows of *P. australis* during low and boom phases of the population cycle of *P. australis*. Active burrows were detected by the presence of recent digging or scats. During each of the 28 sampling sessions, we actively searched for burrows during the day. Specific details of search effort were not kept but averaged 8–10 observer hours per field trip.

Incidental observations.—We recorded all observations of *P. australis* and potential predators—raptors and owls, dingoes (*Canis familiaris*), foxes and cats, and varanid lizards. These observations allowed us to determine whether a species was present during a sampling period despite not being detected during structured surveys.

Predator diet.—We searched for carnivore (dingo, fox, and cat) and native predator scats during all sampling periods. Carnivore scats were distinguished based on size, shape, odor, and color (Triggs 2004). A single scat was defined as 1 or more fecal pellets that appeared to have been deposited in 1

defecation event by a single animal. Only relatively fresh scats that were unbleached by age were collected to ensure that their content reflected current diet. We located the following numbers of fresh scats: 7 dingo, 20 fox, and 3 cat.

Scats were oven-dried at 80°C for 24 h and stored in paper bags prior to analysis. Scats were sent for specialist identification to B. Triggs (Euroa, Victoria, Australia). Each scat was washed through graded sieves to break up prey remains. Prey remains were initially sorted under a dissecting microscope and identified to the lowest taxonomic level possible. The majority of material in scats was mammalian. Mammals were identified to species based on dentaries and hair samples (see Pavey et al. 2008a for details).

Data analysis.—Data analysis was carried out using Statistica version 8.0 (SAS Institute Inc. 2007). We compared changes in abundance of *P. australis* across sites and sampling sessions by calculating the capture rate per 100 trap nights for each sampling session at a site. We calculated the number of individuals captured at each site during each sampling session for comparison across refuge sites. A site was considered to be a refuge for *P. australis* if the species was present there during the majority of sampling sessions during the low phase. We did not use mark–recapture analysis for these data because we did not consider that our sampling frequency was regular enough (Boonstra et al. 2001).

The area of occupancy of *P. australis* during each of the 2 high phases (August 2001–October 2002 and December 2010–May 2011) and the intervening low phase (November 2002–May 2010) was estimated by connecting contiguous locations with evidence of occupation by the species (based on trapping, spotlighting, or burrows) and calculating the area of each of these. The area of each of these locations was then summed for each distinctive phase to give an estimate of the area occupied by *P. australis* within the 7,000-km² study area. Although this method is an estimate only, it was applied consistently across the study and, therefore, should accurately reflect change in area occupied from the 1st high phase to the low phase and then to the following high phase.

We used 2-way analysis of variance (ANOVA) to compare variation in body mass across phase (low versus boom phase) and sex of adults at refuges and also examined the interaction between the 2 variables. The rate of recapture between sessions was low; therefore, we did not use a repeated-measures design. As a consequence, we used body mass data from each individual only once—on the occasion of the 1st capture as an adult (i.e., body mass ≥ 30 g). We log transformed data prior to analysis. Female data consisted of nonreproductive adults (to exclude those in the early stages of pregnancy), whereas we used data for all adult males. Post hoc comparisons between pairs of phase–sex combinations were made using the Tukey honestly significant difference test for unequal sample sizes (Spjøtvoll–Stoline test).

We used 1-way ANOVA to examine variation in proportion of subadults over time at refuge sites during the low phase. We log transformed data prior to analysis. The proportion of subadults was used as a measure of reproductive activity.

We calculated the Pearson product moment correlation to examine whether the 2 abundance measures—capture rate and number of individuals captured—were significantly correlated at each refuge site. We also used this test to examine the relationship between capture rate of *P. australis* and rainfall in the 6 months prior to trapping, capture rate of *P. australis* and index of cat abundance, and capture rate of all rodents and index of raptor abundance. We used a Mann–Whitney *U*-test to examine variation in capture rate between refuge sites during the low phase and outbreak sites during the boom phase. Means $\pm SE$ are given throughout.

We assessed the adequacy of the prey sample size for each species of predator by constructing a randomized cumulative curve for the number of prey taxa occurring against the number of scats sampled. The purpose of this process was to ensure that the sample size of prey individuals was sufficient for the diet to be adequately sampled. The curve was constructed using the program Species Diversity and Richness 4.0 (Seaby and Henderson 2006).

RESULTS

The 11-year study period included only 4 months when mean monthly rainfall was ≥ 100 mm: February 2000, February 2010, October 2010, and February 2011 (Fig. 2). The 2 population irruptions of *P. australis* that occurred during this time took place soon after periods of exceptionally high rainfall. Specifically, *P. australis* underwent a population boom in 2001–2002 with the increase or boom phase of the cycle beginning between May and August 2001 and continuing until October 2002 (Fig. 3). After this phase, populations declined and the low phase of the cycle continued from March 2003 until mid-2010 (Fig. 3) but a 2nd irruption had commenced by the next sampling period in December 2010 (access was limited in the intervening period because of impassable roads).

The changes in population dynamics resulted in the October 2007–May 2011 sampling consisting of 9 sessions with *P. australis* in the low phase and the final 2 sessions with *P. australis* in the boom phase (Fig. 3). During these 11 sampling sessions, abundance (capture rate) of *P. australis* was positively correlated with rainfall in the 6 months prior to trapping ($r = 0.68$, $P = 0.002$). The boom phase during the final 3 sessions was exhibited by all species of rodents in the study area (Pavey and Nano 2013:780, figure 2).

Landscape-scale occurrence.—Over the period of intensive sampling from 2007 to 2011, *P. australis* was recorded at 9 of the 20 monitoring sites during at least 1 of the sampling periods, with 8 sites occupied during the final sampling period (Table 2). Two patterns of site occupation were apparent; 4 sites were occupied during all or the majority of low-phase sampling periods and are considered refuges (Table 2), whereas the remaining sites were either occupied only during the boom phase or, if *P. australis* was recorded during the low phase, occurred in only 1 of the 9 sampling periods. These sites are considered outbreak sites.

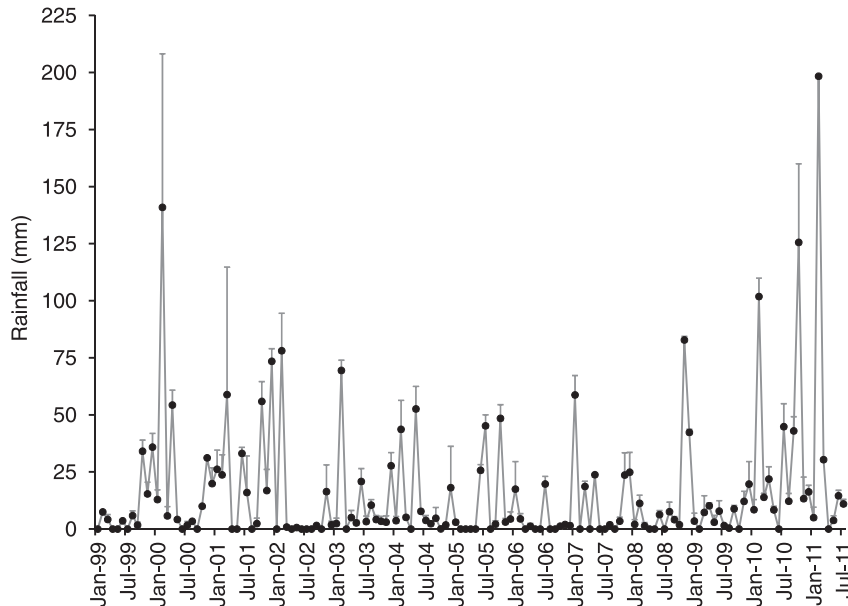


FIG. 2.—Summary of monthly rainfall, mean + SE, from 3 weather stations located in or near Andado Station, Simpson Desert, from January 1999 to July 2011.

The estimated area of occupancy of *P. australis* varied with the phase of the population cycle. Area of occupancy peaked during the boom phases of 2001–2002 and 2010–2011 at 46,600 ha and 56,800 ha, respectively. In contrast, area of occupancy during the low phase was 9,700 ha, which is only 17% of that during the 2010–2011 boom phase.

Population dynamics and reproduction.—The abundance of *P. australis* within and between refuge sites, measured by capture rate and number of individuals captured, varied dramatically across the study period. The pattern of change in capture rate and number of individuals captured over time was significantly correlated for gibber 3 ($r = 0.98$, $P < 0.001$), gibber 2 ($r = 0.98$, $P < 0.001$), and cracking clay 1 ($r = 0.97$, $P < 0.01$), and marginally significant for cracking clay 2 ($r = 0.85$, $P = 0.07$). No significant correlation in the pattern of change in abundance (measured by capture rate) over time occurred for any pair of refuges (Fig. 4; $P > 0.20$ on all occasions). One site (gibber 3) ceased to function as a refuge during the course of the low phase.

Refuge populations of *P. australis* were at high densities during the low phase. The capture rate of these refuge populations was similar to that at outbreak sites during the boom phase. To statistically test this relationship, we compared capture rate for 4 outbreak sites over the 5 sampling periods of the 2000–2002 boom phase (which had a higher capture success than the 2010–2011 boom [Fig. 3]) with that of 3 refuge sites over the last 5 sampling periods of the low phase (March 2009–May 2011). To do this, capture rate for each site was averaged over the 5 sampling periods and those averages were compared for refuge and outbreak sites. There was no statistical difference between the 2 site–phase combinations (refuge low phase: 16.55 ± 4.88 captures/100 trap nights,

outbreak boom phase: 13.97 ± 3.90 captures/100 trap nights; $U = 87.00$, $P = 0.63$).

Refuge populations of *P. australis* maintained body condition during the low phase. Mean body mass (g) of males was refuge low phase 40.28 ± 0.83 ($n = 49$), refuge boom phase 39.88 ± 1.00 ($n = 73$), and outbreak boom phase 37.85 ± 1.86 ($n = 10$). For females it was refuge low phase 35.67 ± 0.80 ($n = 39$), refuge boom phase 36.42 ± 1.27 ($n = 19$), and outbreak boom phase 35.07 ± 2.21 ($n = 7$). Body mass of animals in refuges did not vary significantly with the phase of the population cycle ($F_{1,176} = 0.00$, $P = 0.98$; outbreak sites were excluded from analysis because of low sample sizes). In contrast, sex ($F_{1,176} = 13.73$, $P < 0.001$) had a significant

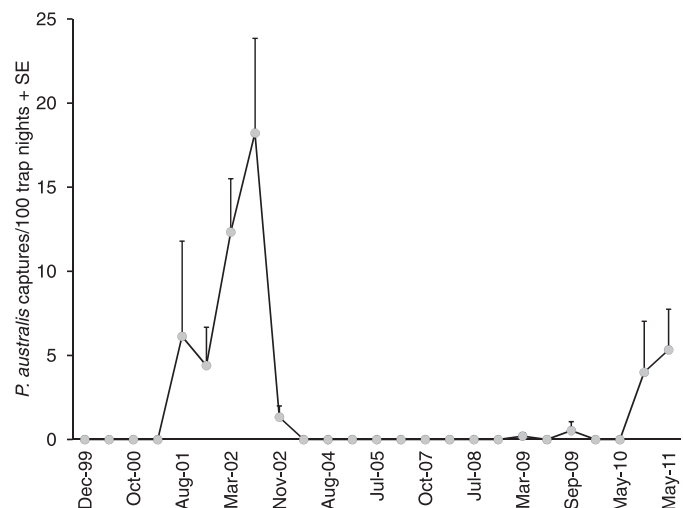


FIG. 3.—Mean capture rate of *Pseudomys australis* + SE at outbreak sites from December 1999 to May 2011, Andado Station, Simpson Desert.

TABLE 2.—The proportion of monitoring sites occupied by the plains mouse (*Pseudomys australis*) during each of 11 sampling periods from October 2007 to May 2011 at Andado Station, Simpson Desert, Australia. ✓ = site was occupied by *P. australis* during the sampling session; NS = site was not sampled during the sampling session.

Site	Sampling period and phase of population cycle																						
	October 2007		April 2008		July 2008		November 2008		March 2009		June 2009		September 2009		February 2010		May 2010		December 2010		May 2011		
	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	Low	Boom	
Gibber 1																							
Gibber 2 ^a			✓				✓		✓		✓		✓		✓		✓		✓		✓		✓
Gibber 3 ^a			✓				✓		✓		✓		✓		✓		✓		✓		✓		✓
Gibber 4																							
Gibber 5							NS																
Gibber 6							NS																
Gibber 7							NS																
Gibber 8							NS																NS
Sand 1																							
Sand 2																							
Sand 3																							
Sand 4																							
Sand 5																							
Sand 6																							
Sand 7																							
Sand 8																							NS
Cracking clay 1 ^a																							
Cracking clay 2 ^a																							
Swamp 1																							
Swamp 2																							
Proportion of sampled sites occupied	0.06		0.11		0.06		0.15		0.25		0.20		0.20		0.15		0.16		0.39		0.50		0.50

^a Refuge site.

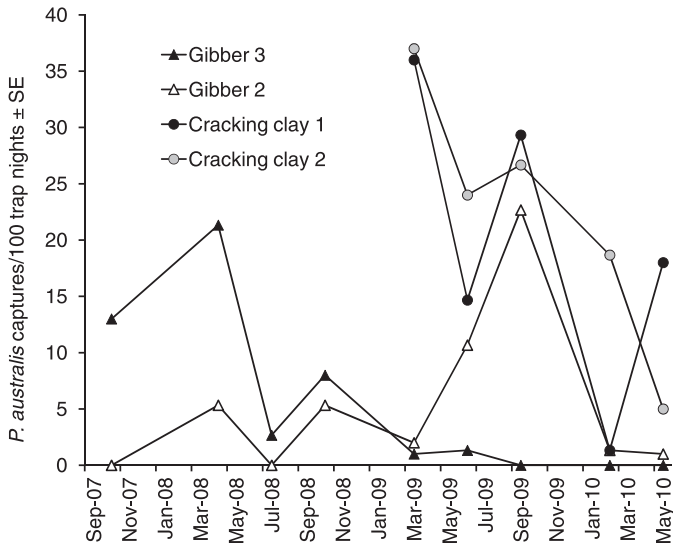


FIG. 4.—Variation in abundance of *Pseudomys australis* at 4 refuges during the low phase of the population cycle from October 2007 to May 2010, Andado Station, Simpson Desert.

influence on body mass, with female body mass in the low phase being significantly lighter than male body mass in both low and boom phases. The interaction between the 2 factors was not significant ($F_{1,176} = 0.48, P = 0.49$).

Refuge populations of *P. australis* continued to breed during the low phase of the population cycle. Subadult *P. australis* were captured in refuges during 5 sampling sessions and contributed more than 20% of captures during sampling in October 2008 and March 2009 (Fig. 5). Variation in the proportion of subadults in refuge sites across the 9 sampling sessions of the low phase was not statistically significant ($F_8 =$

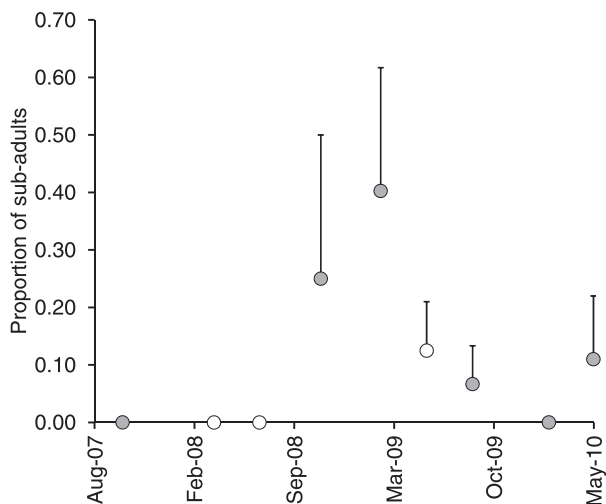


FIG. 5.—Mean proportion of subadult *Pseudomys australis* + SE at 4 refuges during the low phase of the population cycle from October 2007 to May 2010, Andado Station, Simpson Desert. Gray fill indicates the capture of reproductive adults (pregnant or lactating females and scrotal males); white fill indicates no reproduction.

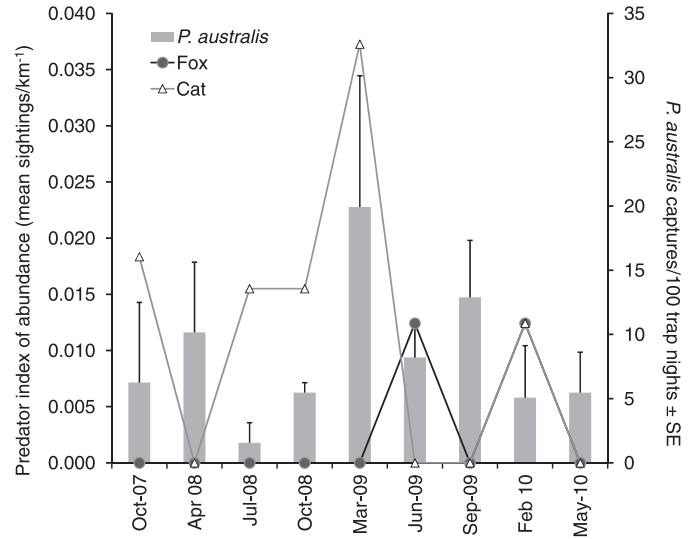


FIG. 6.—Index of abundance of introduced predators, based on spotlight transects, and mean capture rate of *Pseudomys australis* + SE across 4 refuges during the low phase of the population cycle of *P. australis*, October 2007–May 2010, Andado Station, Simpson Desert.

0.93, $P = 0.53$). Reproductive adults were captured during 2 of the 4 sampling periods without subadults.

Native predators: occurrence.—A varanid lizard, *Varanus gouldii*, was widespread but uncommon in the study area, being recorded as incidental sightings and 2 small individuals captured in box traps. It was observed on sand plain, swamp, and, rarely, gibber plain. These sightings indicate that the species was resident in the study area but that it did not occur in the vicinity of any refuges of *P. australis*.

Neither of the specialist arid-zone avian rodent-predators (*T. javanica* or *E. scriptus*) was observed during the low phase of the population cycle despite our carrying out spotlight (80.5 km) and diurnal driving (112.5 km) and walking (10 km²) transects during each of 9 sampling sessions. None of the diurnal raptors detected on survey transects is known to prey on *P. australis*. The index of diurnal raptor abundance was not correlated with the capture rate of rodents (all species) across the 9 sampling periods of the low phase ($r = -0.29, P = 0.45$). We observed 1 nocturnal avian predator, the southern boobook, *Ninox novaeseelandiae*, an owl, during spotlight transects in the low phase (a single bird recorded in May and June 2009).

Introduced predators: occurrence and diet.—The red fox and feral house cat persisted in the study area during the low phase of the cycle of *P. australis* (Fig. 6). Cats were observed during spotlight transects during 5 of the 9 low-phase sampling periods and recorded incidentally during another 2 periods (June 2009 and September 2009). In contrast, foxes were detected during only 2 spotlight sampling periods, although incidental records were obtained during sampling in July 2008 and September 2009. The dingo was not detected during any of the spotlight or diurnal transects; however, incidental observations were made during 6 low-phase sampling sessions from October 2007 to May 2010.

The index of abundance of cats was not correlated with capture rate of *P. australis* across the 9 low-phase sampling periods ($R = -0.06$, $P = 0.88$). However, the peak in the cat abundance index occurred in the same sampling session (March 2009) as the peak in mean capture rate of *P. australis* across the 4 refuges (Fig. 6). The cat sighting rate for this sampling period (0.037 individual/km) was more than double the sighting rate for the next highest sampling period (0.018 individual/km in October 2007). To examine this relationship further, we carried out supplementary spotlighting observations in May 2009 along 2 spotlight transects that traversed the refuges (cracking clay 1 and 2) with high capture rates of *P. australis* during March 2009 (Fig. 4). The sighting rate along these 2 transects in May 2009 was 0.235 individual/km and 0.059 individual/km for cat and fox, respectively.

The randomized cumulative curve of prey taxa reached an asymptote for fox but not cat or dingo. Fox diet ($n = 20$ scats) at the cracking clay refuges during the low phase (June 2009–February 2010) consisted of 30.4% *P. australis* ($n = 23$ individuals), 17.4% other *Pseudomys* species, and 39.1% house mice (*Mus musculus*). Cat diet ($n = 3$ scats) at the same refuges in June 2009 consisted solely of *P. australis* ($n = 3$). Dingo scats ($n = 7$) did not contain any *P. australis*.

We observed foxes and cats actively hunting *P. australis* at night in cracking clay sites 1 and 2 in both May and June 2009. Foxes and cats waited at the entrances of burrows of *P. australis* for individuals to emerge.

DISCUSSION

Our research sought to understand population dynamics of the vulnerable rodent *P. australis* during the low phase of its cycle in a region where introduced predators rather than habitat loss and degradation are the key threats to mammal persistence. We demonstrated that *P. australis* contracts to discrete areas of the landscape during the low phase and that during our study period these refuges occupied a small proportion (17%) of the range occupied during population peaks. This result is similar to that exhibited by rodents in the South American arid zone (Milstead et al. 2007).

Refuges appear to be the main locations occupied for the majority of any given time period; the 138-month duration of our study included a minimum of 108 months (78%) in the low phase of the cycle. Significantly, populations in refuges are in good condition (as assessed by body mass), occur in high density, and reproduce during dry conditions. There was no difference in capture rate between low-phase refuge populations and boom-phase populations at outbreak sites. Native predators are rare or absent during the low phase, whereas cats and foxes persist during drought and prey on refuge populations of *P. australis*.

Our sampling showed that *P. australis* was rarely detectable away from refuges during the low phase. Specifically, we recorded occupation of only 2 outbreak sites, both by a single animal, during 9 low-phase sampling sessions (Table 2). In the case of gibber 3 it is unclear why the site ceased to function as

a refuge after being occupied for 6 consecutive low-phase sampling sessions. The study methodology addressed the more fundamental question of whether refuges occur or not and did not measure changes in resources over time.

Refuges of *P. australis* in our study area and elsewhere across the species' range are typically located on or adjacent to cracking clay plains (Brandle et al. 1999). The clay soils at these locations form wide and deep cracks over an extensive area, thus providing plentiful shelter opportunities and the potential to support high densities of *P. australis*. Refuges are typically run-on areas that support concentrations of ephemeral plants in response to small rainfall events. Rainfall events of 10–20 mm occur on average 4 times per year in the study area (Nano et al. 2013) and these produce responses from shallow-rooted, short-lived grasses and forbs (Nano and Pavey 2013). These plants are the favored food resources of *P. australis* (E. Jeffries, pers. comm.; C. Pavey, pers. obs.). The regular availability of this food resource during drought is likely an important factor in supporting the high density, good body condition, and ongoing reproduction of refuge populations of *P. australis* during droughts.

Notwithstanding the above details of refuges on cracking clay, this study did not seek to provide a clear description of the characteristics of refuge sites. Rather it asked the more fundamental question of whether or not the species uses refuges (1st hypothesis in Table 1). As a consequence, questions regarding the location and characteristics of refuges are outside the scope of the current study but need to be addressed in the near future. Foremost among these will be an autecological study of populations of *P. australis* in refuges during the low phase to identify the key resources present and then to measure change in availability of these over time.

The absence of native predators of *P. australis*, such as raptors and owls, during the low phase was expected because the majority of these species are rodent specialists that themselves have evolved irruptive population dynamics (e.g., Pavey et al. 2008b). Suitable nesting sites also are in low supply for hollow- and tree-nesting birds and they are likely to occupy our study area only during rodent outbreaks. The only other native predator that could capture significant numbers of rodents is the brush-tailed mulgara (*Dasyercus blythi*). This species occurs in the area but it is rare and *P. australis* is outside its prey size range (Pavey et al. 2009, 2011). Because native predators are largely absent during the low phase, it is likely that refuges of *P. australis* naturally experience low levels of predation during drought. In contrast, foxes and cats have a wide prey range that includes invertebrates, reptiles, birds, and carrion (Pavey et al. 2008a; Cupples et al. 2011) and, therefore, can persist in the system during drought. The cumulative frequency curve of fox but not cat reached an asymptote, indicating that dietary sampling was sufficient. However, our dietary results indicate that predation pressure on *P. australis* in refuges can come from both foxes and cats.

An important implication for conservation of *P. australis* from this study is that, given the high density in refuges and the species' large body mass, refuge populations represent

significant concentrations of biomass in a dry and resource-poor environment for cats and foxes. Our contention that refuge populations of *P. australis* are threatened by significant predation pressure from cats and foxes is based on multiple pieces of evidence, including a spike in predator sightings following a peak in abundance of *P. australis* at refuges, direct observations of foxes and cats hunting *P. australis*, and dietary data.

The limited spatial extent of refuges of *P. australis* makes them particularly vulnerable to disturbance. Here, we provide evidence of the likely impact of cat and fox predation; however, other forms of disturbance such as grazing pressure from cattle (*Bos taurus*), European rabbits (*Oryctolagus cuniculus*), and other introduced herbivores (Morton 1990; Johnson 2006) or construction of farming and mining infrastructure (bores, cattle yards, and mineral exploration sites) could represent a threat to refuge populations. Because refuges act as sites from which *P. australis* can disperse and reoccupy other areas during boom periods, predation or other disturbance of refuges during the low phase of cycles can delay the species' ability to build up numbers in response to good conditions. In the medium term, this process threatens the ability of *P. australis* and other declining rodents to persist as the number of suitable refuges declines over time, similar to the model developed by Morton (1990).

An advantage of the limited spatial extent and long duration of occupation of refuges by *P. australis* is that these parts of the landscape emerge as foci for management activities. The relatively small area of refuges increases the chances of successful implementation of management actions to control key threats. Current landscape-scale management (e.g., predator control and prescribed burning) in arid Australia is often difficult to implement and usually operates at a scale that includes large areas of limited conservation value. In contrast to landscape-scale predator management, local-scale control of foxes has been very effective in enabling persistence of remnant populations of rock-wallabies and other threatened mammals (Risbey et al. 2000; Kinnear et al. 2002). This local-scale control has resulted in an increase in population size and in an expansion in the habitats occupied by threatened mammal populations (Kinnear et al. 2002). Such an approach has great potential to reduce the impact of predation by cats and foxes in the vicinity of rodent refuges. Local-scale predator control together with rabbit control and active prevention of other disturbances, such as the placement of infrastructure or bores, can reduce or eliminate threats to refuge populations of declining rodents if undertaken in a systematic manner.

In conclusion, our results lead us to advocate a novel approach to the management of irruptive rodents in arid systems, one that emphasizes detection of the discrete parts of the landscape that function as drought refuges for threatened species and to focus threat management there. This refuge-based approach offers a cost-effective alternative to current property-scale management because it means that intense local-scale management can be used to control threats in the small part of the landscape where it will have maximum impact. A

key advantage of the refuge-based approach is that it offers the potential for off-reserve conservation if refuge location and management can be effectively communicated to land managers. The inadequate protection of threatened species within Australia's protected-area system highlights the need for such alternative approaches (Watson et al. 2011).

ACKNOWLEDGMENTS

Financial support was provided by the Northern Territory Natural Resource Management Board. We thank D. and C. Costello for allowing us unrestricted access to both Andado Station and New Crown Station. We thank J. and L. Spencer for hospitality during our early stays at Old Andado. We are grateful for the field assistance provided by K. McConnell, S. Raghu, R. Povey, J. Ford, P. Nunn, G. Fyfe, A. Nano, A. James, A. Schubert, A. Graham, M. Heywood, G. Horne, C. Smith, and a number of Northern Territory Parks and Wildlife rangers. Predator scats were analyzed by B. Triggs. We thank S. Raghu and S. Morton for constructive comments on the manuscript. Ethics approval was obtained from Charles Darwin University Animal Ethics Committee (A07010).

LITERATURE CITED

- BOONSTRA, R., C. J. KREBS, S. GILBERT, AND S. SCHWEIGER. 2001. Voles and mice. Pp. 215–239 in *Ecosystem dynamics of the boreal forest: the Kluane project* (C. J. Krebs, S. Boutin, and R. Boonstra, eds.). Oxford University Press, Oxford, United Kingdom.
- BRANDLE, K. E. MOSEBY, AND R. M. ADAMS. 1999. The distribution, habitat requirements and conservation status of the plains rat *Pseudomys australis* (Rodentia: Muridae). *Wildlife Research* 26:463–477.
- BRANDLE, R., AND K. E. MOSEBY. 1999. Comparative ecology of two populations of *Pseudomys australis* in northern South Australia. *Wildlife Research* 26:541–564.
- BRANDLE, R., AND C. R. PAVEY. 2008. Plains rat *Pseudomys australis*. Pp. 616–618 in *The mammals of Australia* (S. M. van Dyck and R. Strahan, eds.). 3rd ed. New Holland Publishers, Sydney, Australia.
- BURBIDGE, A. A., AND N. L. MCKENZIE. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* 50:143–198.
- BURBIDGE, A. A., ET AL. 2008. Conservation status and biogeography of Australia's terrestrial mammals. *Australian Journal of Zoology* 56:411–422.
- CARDILLO, M., G. M. MACE, J. L. GITTLEMAN, AND A. PURVIS. 2006. Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences* 103:4157–4161.
- CUPPLES, J. B., M. S. CROWTHER, G. STORY, AND M. LETNIC. 2011. Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *Journal of Mammalogy* 92:590–600.
- DICKMAN, C. R., A. C. GREENVILLE, C.-L. BEH, B. TAMAYO, AND G. M. WARDLE. 2010. Social organization and movements of desert rodents during population "booms" and "busts" in central Australia. *Journal of Mammalogy* 91:798–810.
- DICKMAN, C. R., A. C. GREENVILLE, B. TAMAYO, AND G. M. WARDLE. 2011. Spatial dynamics of small mammals in central Australian desert habitats: the role of drought refugia. *Journal of Mammalogy* 92:1193–1209.

- JOHNSON, C. N. 2006. Australia's mammal extinctions: a 50 000 year history. Cambridge University Press, Melbourne, Australia.
- JOSEPH, L. N., S. A. FIELD, C. WILCOX, AND H. P. POSSINGHAM. 2006. Presence-absence versus abundance data for monitoring threatened species. *Conservation Biology* 20:1679–1687.
- KINNEAR, J. E., N. R. SUMNER, AND M. L. ONUS. 2002. The red fox in Australia—an exotic predator turned biocontrol agent. *Biological Conservation* 108:335–359.
- LETNIC, M., P. STORY, G. STORY, J. FIELD, O. BROWN, AND C. R. DICKMAN. 2011. Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy* 92:1210–1222.
- MCKENZIE, N. L., ET AL. 2007. Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* 34:597–611.
- MILSTEAD, W. B., P. L. MESERVE, A. CAMPANELLA, M. A. PREVITALI, D. A. KELT, AND J. R. GUTIÉRREZ. 2007. Spatial ecology of small mammals in north-central Chile: role of precipitation and refuges. *Journal of Mammalogy* 88:1532–1538.
- 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.
- NANO, C. E. M., A. E. BOWLAND, T. J. NANO, S. RAGHU, AND C. R. PAVEY. 2012. Demographic hurdles to persistence in *Acacia peuce* (F. Muell.): Effects of resources, fire and browsing on a threatened keystone tree species from arid Australia. *Journal of Arid Environments* 80:17–26.
- NANO, C. E. M., A. E. BOWLAND, AND C. R. PAVEY. 2013. Factors controlling regeneration in a rare desert tree *Acacia peuce*: limits to soil seed bank accumulation in time and space. *Journal of Arid Environments* 90:114–122.
- NANO, C. E. M., AND C. R. PAVEY. 2013. Refining the 'pulse-reserve' model for arid central Australia: seasonal rainfall, soil moisture, and plant productivity in sand ridge and stony plain habitats of the Simpson Desert, Australia. *Austral Ecology* 38:741–753.
- OSTFELD, R. S., AND F. KEESING. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution* 15:232–237.
- PAVEY, C. R., C. J. BURWELL, G. KÖRTNER, AND F. GEISER. 2009. Incorporation of vertebrates in the diet decreases winter torpor use in a desert marsupial. *Naturwissenschaften* 96:679–683.
- PAVEY, C. R., S. R. ELDRIDGE, AND M. HEYWOOD. 2008a. Native and introduced predator population dynamics and prey selection during a rodent outbreak in arid Australia. *Journal of Mammalogy* 89:674–683.
- PAVEY, C. R., J. GORMAN, AND M. HEYWOOD. 2008b. Dietary overlap between the nocturnal letter-winged kite *Elanus scriptus* and barn owl *Tyto alba* during a rodent outbreak in arid Australia. *Journal of Arid Environments* 72:2282–2286.
- PAVEY, C. R., AND C. E. M. NANO. 2013. Changes in richness and abundance of rodents and native predators in response to extreme rainfall in arid Australia. *Austral Ecology* 38:777–785.
- PAVEY, C. R., C. E. M. NANO, S. J. B. COOPER, J. R. COLE, AND P. J. McDONALD. 2011. Habitat use, population dynamics and species identification of mulgara, *Dasyercus blythi* and *D. cristicauda*, in a zone of sympatry in central Australia. *Australian Journal of Zoology* 59:156–169.
- PREVITALI, M. A., M. LIMA, P. L. MESERVE, D. A. KELT, AND J. R. GUTIÉRREZ. 2009. Population dynamics of two sympatric rodent species in a variable environment: rainfall, resource availability, and predation. *Ecology* 90:1996–2006.
- QUIN, D. G., AND A. P. SMITH. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* 77:243–267.
- RISBEY, D. A., M. C. CALVER, J. SHORT, J. S. BRADLEY, AND I. W. WRIGHT. 2000. The impacts of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* 27:223–235.
- SAS INSTITUTE INC. 2007. SAS/STAT user's guide. Release 8.0. SAS Institute Inc., Cary, North Carolina.
- SEABY, R. M., AND P. A. HENDERSON. 2006. Species Diversity and Richness. Version 4. Pisces Conservation International, Lynton, United Kingdom.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- STAPP, P. 2010. Long-term studies of small mammal communities in arid and semiarid environments. *Journal of Mammalogy* 91:773–775.
- TRIGGS, B. 2004. Tracks, scats and other traces: a field guide to Australian mammals. Oxford University Press, Melbourne, Australia.
- VAN ETEN, E. J. B. 2009. Inter-annual rainfall variability of arid Australia: greater than elsewhere? *Australian Geographer* 40:109–120.
- WATSON, J. E. M., ET AL. 2011. The capacity of Australia's protected-area system to represent threatened species. *Conservation Biology* 25:324–332.
- WILSON, K. A., ET AL. 2012. Prioritizing conservation investments for mammal species globally. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 366:2670–2680.
- WOJNARSKI, J. C. Z., ET AL. 2011. The disappearing mammal fauna of northern Australia: context, cause and response. *Conservation Letters* 4:192–201.

Submitted 24 July 2013. Accepted 6 November 2013.

Associate Editor was Loren D. Hayes.