Biodiversity and Conservation (2025) 34:3071–3087
https://doi.org/10.1007/s10531-025-03113-x

ORIGINAL RESEARCH

A population irruption of the long-haired rat, *Rattus villosissimus*, brings rare trophic interactions to the Simpson desert, Australia

Chris R. Pavey[1] · S. Raghu[2] · Gerhard Körtner[3] · Catherine E. M. Nano[4]

Received: 18 February 2025 / Revised: 4 June 2025 / Accepted: 6 June 2025 /
Published online: 21 June 2025
© Crown 2025

Abstract
Species with irruptive population dynamics, that undergo dramatic outbreaks during which they invade normally unoccupied areas, provide a useful template with which to view rare or novel species interactions. Here we document biotic interactions during a population irruption of the long-haired rat (*Rattus villosissimus*) into the Simpson Desert, Australia. The rat is the largest extant rodent in arid Australia (average body mass: 134 g) being 3–4 times heavier than resident rodents. The study examined direct predation on and/or displacement of resident rodent species (using 21 years of monitoring data, 1999–2020) and examined if browsing caused damage and/or mortality of the sapling population of the dominant tree *Acacia peuce* (using 40 years of monitoring (1979–2019) of a sapling population of 146 individuals). Over 21 years, all but three records of *R. villosissimus* were during a period of 31 months (June 2010 to December 2012). Three distinct effects of the rats on the ecosystem were detected, specifically, potential displacement of resident rodent populations (*Notomys alexis*, *Pseudomys australis*) by *R. villosissimus*, direct predation on other rodents, and browsing impacts on *A. peuce* that ranged from moderate through severe damage to outright mortality in 7% of monitored saplings. The rare interactions produced by the rat outbreak did not have lasting effects on small mammals. By contrast, *A. peuce* sapling vigour and population growth may be negatively impacted by *R. villosissimus* should outbreaks occur more frequently as a result of changing climate.

Keywords *Acacia peuce* · Herbivory · Keystone · Population dynamics · Predation

Communicated by Nigel Stork

✉ Chris R. Pavey
chris.pavey@csiro.au

[1] CSIRO Environment, Brisbane, QLD, Australia

[2] CSIRO Health and Biosecurity, Brisbane, QLD, Australia

[3] Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW, Australia

[4] Flora and Fauna Division, Department of Environment, Parks and Water Security, Northern Territory Government, Northern Territory, Alice Springs, Australia

Introduction

Species with irruptive population dynamics periodically undergo dramatic outbreaks during which time they increase geographic range and move into areas that are otherwise not occupied (Pavey et al. 2017). Such events are rare in space and time but occur when primary productivity is high driving high rates of reproduction and survival as a consequence of plentiful food availability (White 2019). One of the outcomes of these movements is the emergence of biotic interactions between species that normally have allopatric ranges. This situation creates novel trophic interactions and potentially affects the functioning of food webs. Such interactions, though temporary, can provide insights into novel interactions resulting from introductions of non-natives or when species tracking a changing climate (and formerly with allopatric ranges) share space for the first time (Loarie et al. 2009; Kechnebbou et al. 2021). Rare trophic interactions resulting from irruptive dynamics have the potential to negatively impact the resident biota through increased competition for space and resources, predation, and herbivory (Kelt 2011). Currently there is limited information on the prevalence, strength or outcome of rare trophic interactions.

The rodent genus *Rattus* (Muridae) has several species that are suitable candidates for assessment of this phenomenon. Multiple Australian species in the genus are irruptive (Redhead 1979; Madsen and Shine 1999; Madsen et al. 2006; Short et al. 2018) and they are known to interact negatively with agriculture and forestry during population outbreaks (Braithwaite and Griffiths 1996; Hunt et al. 2012). The endemic long-haired rat, *Rattus villosissimus* (maximum body mass, 280 g), inhabits arid and semi-arid environments of northern Australia, a region that experiences highly unpredictable rainfall (McMahon et al. 2008; van Etten 2009). When extreme rainfall events (i.e. annual rainfall > 750 mm) do occur, the species can undergo dramatic increases in population size (Crombie 1944; Carstairs 1974; Greenville et al. 2013). During some of these events individuals move long distances along the channels of drainage lines invading geographical areas that are not otherwise occupied including the Simpson Desert, central Australia (Newsome and Corbett 1975; Predavec and Dickman 1994; Greenville et al. 2013; Pavey and Nano 2013). The colonisation of sites beyond the normal range of the species is rare (occurring at intervals of 25–30 years) compared to the frequency of the irruption events of resident species of rodents (every 8–10 years) (Dickman et al. 1999; Greenville et al. 2016; Stringer et al. 2024).

The appearance of a large native rodent such as *R. villosissimus* in high numbers is predicted to change the functioning of ecosystems in several ways for the period the species is present and into the future. Specifically, the species is three to four times larger than resident rodents in the Simpson Desert (Table 1), therefore, it is likely to be a superior competitor for food and habitat resources. Further, predator-prey interactions would likely be altered given the increase in rodent biomass available to predators when *R. villosissimus* is present in high abundance. *Rattus villosissimus* could potentially also predate on smaller rodents and other small mammals. In addition, the burrowing of *R. villosissimus* is a source of movement of significant amounts of soil in an environment where most other burrowing species are now extinct. Further, rodents are known worldwide to be significant sources of seed predation and seedling herbivory (e.g. Bowman et al. 2017) and this is the case with several *Rattus* species in Australia (Braithwaite and Griffiths 1996). Thus, the irruption of this species may cause an alteration of 'bottom up' and 'top down' trophic interactions as well as changes to the physical environment.

Table 1 A list of each species of rodent captured in the study area on Andado and New Crown Stations in the western Simpson Desert, Australia, from 1999 to 2020 showing mean body mass, number of captures, and capture rate for each species. Body mass data are from Van Dyck and Strahan (2008)

Species	Mean body mass (g)	Number of captures	Overall capture rate (captures/100 trap nights)
Leggadina forresti	20	2	< 0.01
Mus musculus	13	854	1.65
Notomys alexis	35	855	1.65
Pseudomys australis	40	1,669	3.22
P. hermannsburgensis	12	1,315	2.54
P. desertor	25	5	0.01
Rattus villosissimus	134	349	0.67
Total		5,049	9.74

Here, we report on the rare biotic interactions that resulted from the geographic expansion of *R. villosissimus* into the western Simpson Desert during a population irruption in response to extreme rainfall in 2010 and 2011 (Wardle et al. 2013). This outbreak was the first reported for the study area since the 1970s (Newsome and Corbett 1975). Our aim in this study is to examine the hypothesis that the temporary appearance of a large native rodent will change the functioning of a regional ecosystem. We focussed on two sets of biotic interactions. Specifically, to address whether *R. villosissimus* becomes a significant competitor and predator of native rodents during irruptions, we examined changes in abundance of native rodents during irruptive events. We also collated anecdotal evidence of predation by *R. villosissimus* on smaller species. Second, we assessed the impact of herbivory by *R. villosissimus* on the demography (mortality and stem kill) of a threatened keystone plant at the site, *Acacia peuce*, a perennial tree used extensively by birds as nesting and roosting sites.

Methods

Study area

The study was undertaken on Andado Station and New Crown Station in the Simpson Desert, southeast of Alice Springs, Northern Territory, Australia. The regional climate is dominated by long periods with low rainfall and daily extremes in temperature. Average annual rainfall based on three weather stations in the vicinity of the study area is 154 mm (Pavey et al. 2014). The region's climate features an irregular periodicity and low predictability of rainfall. More details of the climate and the pattern of rainfall in the study area are provided by Nano et al. (2013).

Occurrence and abundance of rodents including *Rattus villosissimus*

To test the hypothesis that the species is non-resident and occurs at the site on a rare and stochastic basis, we assessed presence and abundance of rodents in the study area from 1999 to 2020 during two monitoring programs (that involved repeated trapping of permanent sites) and five survey trips (that involved sampling a range of habitats in an effort to locate target species including *R. villosissimus*). All trapping involved the use of aluminium box traps (Elliott Scientific, Upwey, Victoria).

The first monitoring program ran from 1999 to 2007 on 11 sites, with each site consisting of a line of either 25 or 50 box traps spaced 10–15 m apart (see Pavey et al. 2008 for further details). The sites were trapped on 17 occasions with 2 to 6 sites being trapped during each monitoring session for three or, rarely, two nights for a total of 5,750 trap nights. The second monitoring program involved trapping 20 permanent grids with each grid consisting of 25 box traps set in a five by five array with 20 m between adjacent traps. Grids were placed in a northern and southern block with each block consisting of grids located in three main habitat types as follows: (1) gibber plain, (2) clay plain (including cracking clay plain and swamp) and (3) sand habitat (including sandridge and sand plain). Trapping was carried out from October 2007 to September 2020. Traps were left open for three to four nights per session. Sites were trapped 24 times for a total of 32,720 trap nights (see Pavey 2021 for further details). All trapping during the two monitoring programs involved the use of a mixture of peanut butter and rolled oats as bait.

Survey trips were carried out in May and July 2008, May and June 2009, and October 2013. Details of the trapping are provided in Pavey et al. (2011); briefly, these consisted of 49 trap sites with each site trapped on at least one occasion. Forty-five sites consisted of a grid of box traps (set as for the permanent sites, above) and open for two to four nights of which the habitat was located on sandridge (18), sand plain (2), gibber plain (7), clay plain (13), and swamp (5). These traps were baited with a mixture of peanut butter and rolled oats. An additional four sites were set on extensive areas of gibber plain that consisted of a long line of box traps set in pairs with adjacent pairs 100 m apart. The length of these lines was 7.4 km, 7.4 km, 4.8 km and 1.8 km, respectively. These lines were open for three to four nights and baited with tinned sardines.

In addition, we carried out trapping during the period that *R. villosissimus* was potentially irrupting in the south of the study area during winter 2010. This effort involved 48 nights of trapping using box and pitfall traps across 31 sites from 21 May to 13 July 2010 for a total of 7,750 trap-nights. Sites were open for between two and 21 nights per site.

We follow Greenville et al. (2013) in considering any *R. villosissimus* with a body mass <60 g as juvenile. Individuals with body mass from 60 to 100 g were classed as sub-adults with adults being >100 g.

Rodent biomass

The biomass of rodents at a site during a sampling session was calculated by multiplying the minimum number of individuals of a species captured during a sampling session by the average body mass of the species (from Table 1). The species specific biomasses at a site were then summed to give the total score for a site. Individuals were temporarily marked to enable identification of recaptures within a sampling session. Marking was either by clipping fur on the hindquarters or marking the tail with a black pen.

Predation of other rodents by *Rattus villosissimus*

Records of *R. villosissimus* capturing and consuming other rodents was obtained from two sources. First, we sought direct observations of predation by observing individual *R. villosissimus* at night. These observations were opportunistic. Second, we recorded any instances when *R. villosissimus* was present in a box trap with another species of rodent that had been

partially consumed. In these instances, we assumed that the *R. villosissimus* had 'forced' itself into the trap after becoming aware that another rodent was already present.

Mortality and damage of *Acacia peuce*

Acacia peuce is listed nationally as Vulnerable under the *Environment Protection and Biodiversity Conservation Act* of 1999. Only three populations are known across the entire range. The population of *A. peuce* in the Northern Territory is distributed within an area of 337 km^2 on Andado Station (Nano et al. 2013) and is estimated at about 2,000 individuals (Raghu et al. 2013). The entire distribution of the species in the Northern Territory is included within our study area.

In September 1979, a total of 13 permanent plots each 25 m by 25 m were established across the population of *A. peuce* with the aim of monitoring the fate of recently established seedlings (Nano et al. 2012). All small plants (< 0.3 m tall) were individually tagged and these, along with any new seedlings that emerged thereafter, were monitored on 26 occasions from September 1979 to February 2011. Subsequently, the plots were monitored on six occasions during and after the outbreak of *R. villosissimus*; May 2011, June 2012, May 2013, May 2015, July 2016 and April 2019. In addition, survivorship of a subsection of plots was assessed in December 2011, when damage to plants was first noted during incidental observations. At this time all individuals in the plots were in either of two juvenile classes recognised by Raghu et al. (2013); 'Sapling 1' and 'Sapling 2'. Each of these individuals was <4 m in height.

During each of the 32 visits from 1979 to 2019, the plots were searched for the tagged plants and for any new individuals, and status was recorded as alive, dead or new. The height of each individual was measured. During the visits from May 2011 to April 2019, we assessed: (a) whether each individual had been damaged by *R. villosissimus*, (b) the location of damage to the stem of the plant as either 'basal', 'mid' or 'upper' and (c) the severity of damage as 'moderate' or 'severe'. Leaf vigour was also assessed. Damage was ascribed to *R. villosissimus* based on visual sign. Specifically, the presence of rat scats and/or burrows at the base of the saplings or in the immediate vicinity of them was treated as causal evidence of observed stem damage. Notably, the likelihood that any other species was responsible for the damage was negligible given that there was no direct or indirect observations of visits to the saplings and that no such damage had previously been recorded outside of the *R. villosissimus* irruption event despite other species irrupting in the area (see Results). Damage ranged from partial bark stripping through to ringbarking and, on occasion, complete stem severance.

Results

During the 21 years of the study (1999–2020), a total of 51,845 trap nights were completed. This trap effort produced captures of 5,049 rodents (including recaptures) at a capture rate of 9.74 animals per 100 trap nights (Table 1).

Presence of *Rattus villosissimus*

The first record of *R. villosissimus* during the current study was on 5 April 2002 in the north of the study area. This capture, of an adult male (body mass: 134 g) occurred during the first monitoring program (described above) and it was at a site located within the main stand of *A. peuce*. The capture occurred during the high phase of a rodent population irruption (Fig. 1) that was driven by plains mouse (*Pseudomys australis*), sandy inland mouse (*P. hermannsburgensis*) and spinifex hopping mouse (*Notomys alexis*) but not house mouse (*Mus musculus*) (Pavey et al. 2008).

Rattus villosissimus was not captured between April 2002 and June 2010 despite a high trap effort on both monitoring grids and survey sites. No further observations were made until a population irruption during 2010–2012. The first animal detected at the onset of the irruption was on 1 June 2010 in the south of the study area. *Rattus villosissimus* was not detected on monitoring grids in May 2010 but it was present during the next monitoring session in December 2010. During the intervening period, almost continuous trapping was carried out from 21 May to 12 July 2010 in the southern block of the study area around Old Andado homestead and including two of the clay monitoring sites. Rats were captured from 1 June until 12 July 2010, when trapping ceased. By the monitoring session in December 2010, *R. villosissimus* was present at both clay sites and one sand site in the south but not on gibber sites. It was also present on one sand site in the north but not on clay or gibber sites. By May 2011, the species was present on all sand and gibber sites trapped in the south (clay sites could not be trapped because they were flooded). In the north, *R. villosissimus* occupied all clay and sand sites and three of the four gibber sites by May 2011.

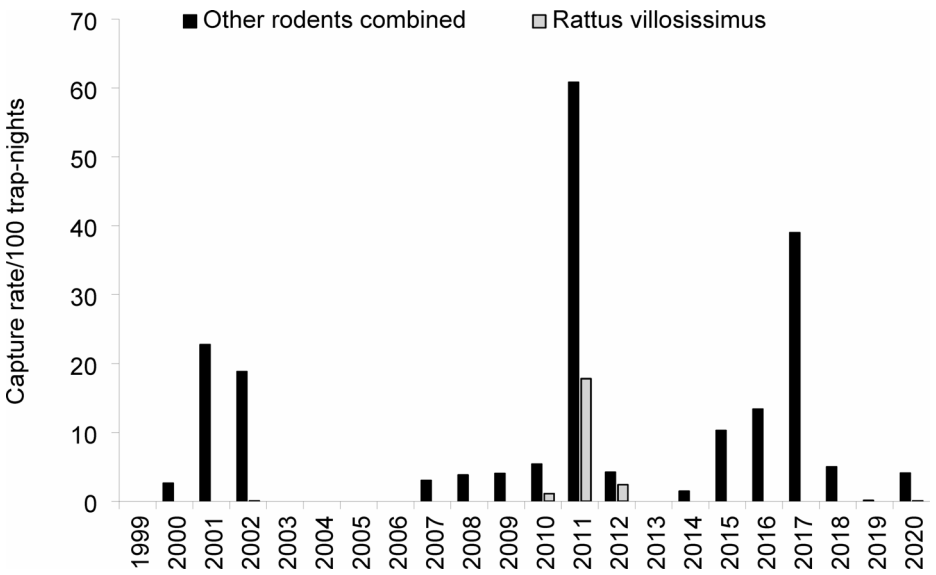


Fig. 1 Capture rate of *Rattus villosissimus* and other rodents combined across the 21-year study period on Andado and New Crown Stations in the western Simpson Desert, Australia, from 1999 to 2020. The capture rate for each year is presented for all trapping sites (monitoring and survey) combined. A single *R. villosissimus* was captured in 2002 and 2020

Trapping was discontinued after the May 2011 sampling session because predation by *R. villosissimus* on other rodents in traps was observed (see below). Trapping resumed in December 2012, but only on the north block, with *R. villosissimus* persisting on two gibber sites but not on clay or sand. No animals were detected on the subsequent sampling trips in early March 2013 (south sites only) and June 2013 (north sites only).

No further individuals were trapped from 13 December 2012 until September 2020 when a single sub-adult female (body mass: 66 g) was trapped in a swamp beside Old Andado homestead (the same location where the species was first detected in June 2010). In addition, a single *R. villosissimus* was recorded in a pellet of a letter-winged kite collected in the north block of the study area on 14 October 2016 (Pavey 2021).

In summary, over a 21-year (251 month) study period, all but three records of *R. villosissimus* were during a period that had a minimum duration of 31 months from June 2010 to December 2012 (Fig. 1). Apart from the two records of single animals (2002 and 2020) the species was detected on the trapping sites only during three years of the 21-year study period (Fig. 1).

Reduction of *Notomys alexis* and *Pseudomys australis* captures during presence of *Rattus villosissimus*

During the second monitoring program (2007–2020), two separate population outbreaks of rodents occurred in the study area. During the first outbreak in 2010–2011, *R. villosissimus* was present whereas during the second outbreak in 2016–2017, *R. villosissimus* was absent (Fig. 1).

A comparison of time series of capture rates in the sand sites (combined across north and south) shows that in 2010–2011, *R. villosissimus* and *N. alexis* occurred in similarly low abundance in December 2010 whereas by May 2011, *R. villosissimus* was dominating captures (Fig. 2a). In contrast, during 2016–2017 with *R. villosissimus* absent, captures of *N. alexis* increased steadily up to 50.10 ± 6.35 SE captures per 100 trap nights by July 2017. This peak did not occur in 2010–2011 (Fig. 2b).

A comparison of time series of capture rates in three of the drought refuge sites (*sensu* Pavey et al. 2025) of *P. australis* show that capture rates declined dramatically from December 2010 (71.11 ± 20.26 captures/100 trap nights) to May 2011 (15.11 ± 7.75 captures/100 trap nights). This unexpected decline in *P. australis* captures was correlated with the appearance of *R. villosissimus* by May 2011 (the species was not detected in December 2010) (Fig. 3a). *Rattus villosissimus* had a higher capture rate than *P. australis* by this time (17.78 ± 4.44 captures/100 trap nights). In contrast, during 2016–2017 with *R. villosissimus* absent, captures of *P. australis* again peaked above 70 captures per 100 trap nights (73.52 ± 1.72) in October 2016 and March 2017 and remained above 50 captures (55.46 ± 21.18 captures) in July 2017 (Fig. 3b).

Rodent biomass

Mean rodent biomass varied across the three sampling periods in both 2010–2011 and 2016–2017 (Fig. 4). On the sand sites it peaked at 2.44 kg/site in May 2011 when *R. villosissimus* was common (Fig. 4) and did not rise above 1.00 kg/site during the other five capture periods despite the high capture rate of *N. alexis* in 2016–2017 (Fig. 2b). On the refuge sites

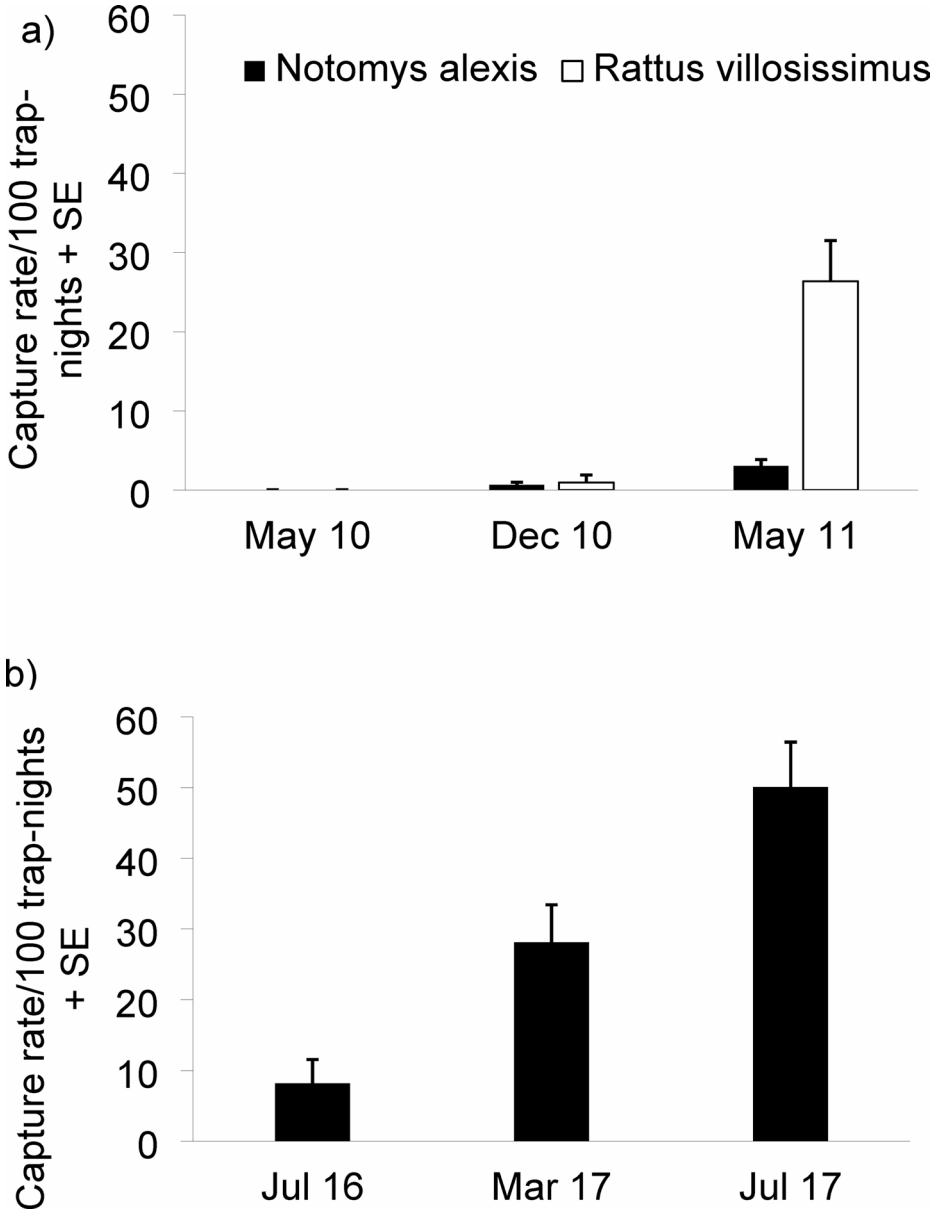


Fig. 2 Time series of capture rate (per 100 trap-nights) of *Notomys alexis* and *Rattus villosissimus* on monitoring grids in sand habitat (combined across all sand sites, N = 8) in the western Simpson Desert, Australia, in: (**a**) 2010–2011 and (**b**) 2016–2017

the presence of *P. australis* alone led to a mean biomass of 2.04 kg/site in December 2010 and 1.81 kg/site in March 2017 (Fig. 4b). Similar to the sand sites, mean biomass at refuge sites was highest in May 2011 (at 2.25 kg/site) when *R. villosissimus* was the most abundant rodent (Fig. 3a).

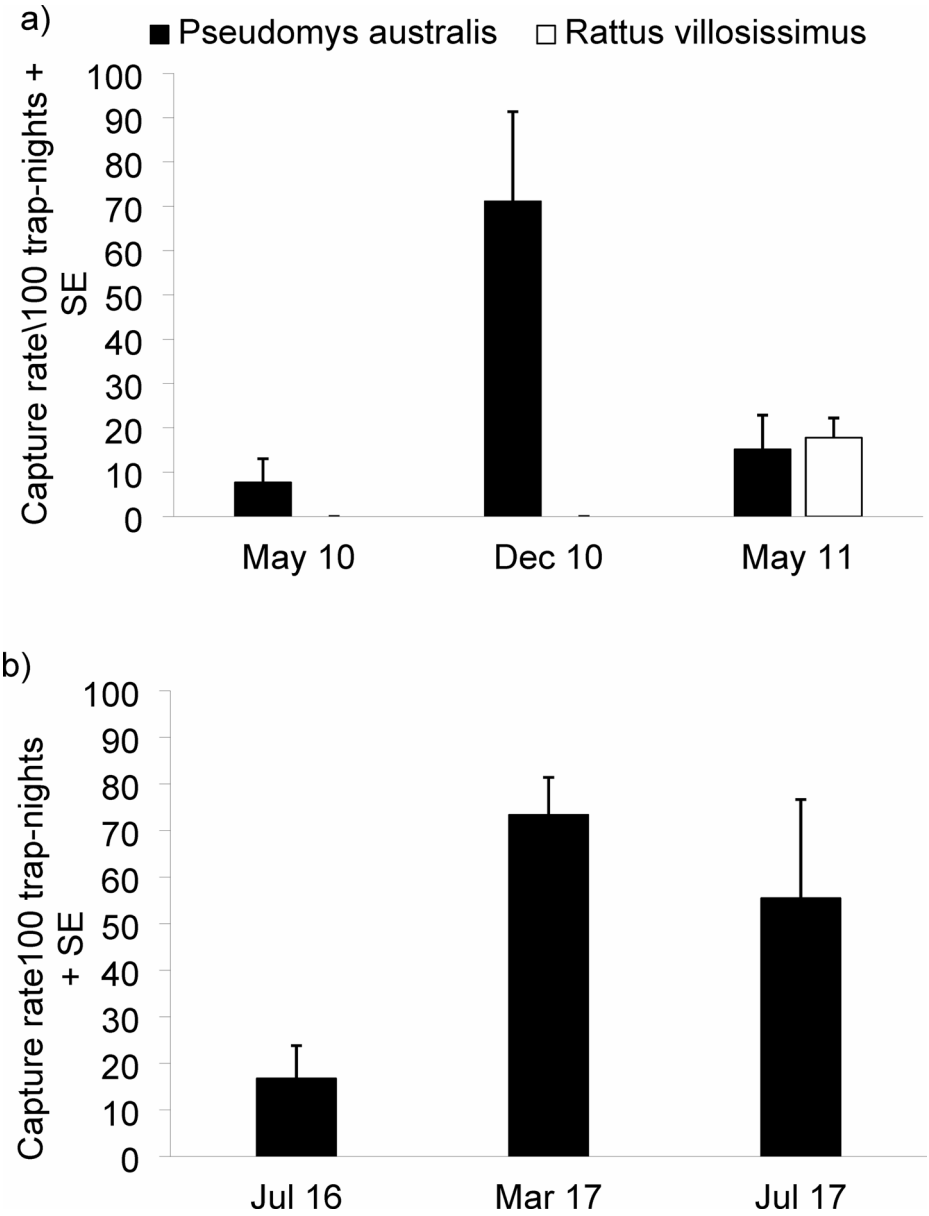


Fig. 3 Time series of capture rate (per 100 trap-nights) of *Pseudomys australis* and *Rattus villosissimus* on monitoring grids in three refuges of *P. australis* in the western Simpson Desert, Australia, in: (**a**) 2010-2011 and (**b**) 2016-2017

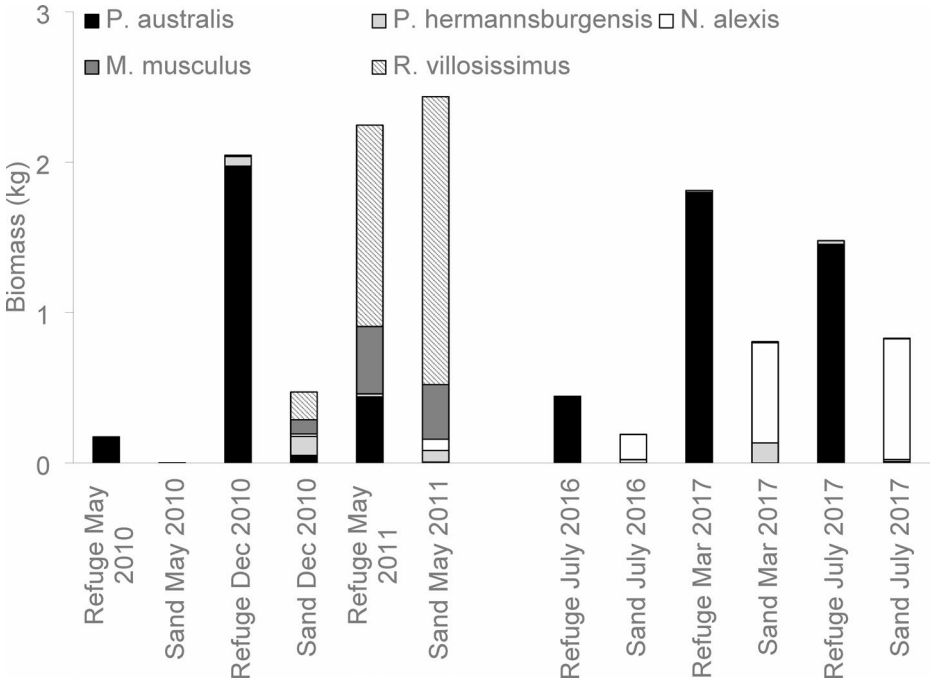


Fig. 4 Mean biomass of the five rodent species (*Pseudomys australis*, *P. hermannsburgensis*, *Notomys alexis*, *Mus musculus*, *Rattus villosissimus*) during three monitoring periods each in 2010–2011 and 2016–2017 in refuges of *P. australis* ($N = 3$) and in sand habitat (combined across all sand sites, $N = 8$) in the western Simpson Desert, Australia. The data are means across all grids trapped during the sampling period

Rattus villosissimus predation on other rodents

Observations and circumstantial evidence of predation by *R. villosissimus* on other rodents was obtained during fieldwork in May 2011 (Table 2). Evidence included both direct observations of predation by *R. villosissimus* on *M. musculus* and instances when *R. villosissimus* was present in a box trap with partially consumed *M. musculus*.

Mortality and damage of *Acacia peuce* saplings by *Rattus villosissimus*

In two of the 14 monitoring plots of *A. peuce*, 100% of saplings were damaged by *R. villosissimus*. The rats damaged the basal, mid and upper stems of saplings (Fig. 5). Rats climbed saplings to access foliage and bark. Damage inflicted on *A. peuce* saplings by *R. villosissimus* included feeding on bark and on new growth of leaves. Some plants had been ring-barked or had suffered dead branches.

Of the two plots that sustained damage, one plot was in the main stand ($N = 41$ saplings monitored since 1982) and the other plot was in an outlying fragment stand ($N = 6$ saplings monitored since 1982). In total, 149 saplings were monitored across the 14 plots, of which 31.5% (47) were damaged by *R. villosissimus*.

Table 2 Observations of *Rattus villosissimus* carnivory obtained during fieldwork in 2011 in the western Simpson Desert, Australia

Date	Habitat	Observation
22 May 2011	Cracking clay– north	Male *R. villosissimus* (270 g) in a trap with a partly consumed *M. musculus*.
24 May 2011	Old Andado homestead	Free-ranging adult *R. villosissimus* observed capturing and consuming an adult *M. musculus*.
25 May 2011	Old Andado homestead	Free-ranging adult *R. villosissimus* observed chasing and pouncing at an adult *M. musculus* that evades capture.
25 May 2011	Old Andado homestead	Free-ranging adult *R. villosissimus* seen feeding on a *M. musculus*.
27 May 2011	Sand - south	Male *R. villosissimus* (not weighed) in a trap with a partly consumed *M. musculus*.

By April 2019, 10 of the 47 damaged saplings had died. Seven of these had died during the rat outbreak (by December 2011). The mortality rate in the year of the rat damage was 7 times higher than background levels over 27.5 years of monitoring pre-2011 (Table 3). Rats had chewed through the main stem and killed one sapling. Pre- and post-event sapling monitoring confirmed that very high sapling survival rates occurred in the absence of rat browsing (Table 3).

Discussion

Over a period of 21 years (1999–2020) we recorded a single irruption and movement of *R. villosissimus* into our study area over a minimum duration of 31 months from June 2010 to December 2012. By comparison, the commonest resident species in the study area, *P. australis* and *N. alexis*, underwent three population outbreaks during this period. Although there is not a continuous record of rodent population dynamics from the western Simpson Desert, the previous recorded population outbreak of *R. villosissimus* occurred in the 1970s (Newsome and Corbett 1975). Monitoring in the eastern Simpson Desert was continuous from 1990 to 2020. Two outbreaks of *R. villosissimus* occurred there during this time; one in 1991–1992 (Predavec and Dickman 1994), another in 2010–2011 (Greenville et al. 2013). These observations from long-term monitoring show that movement of *R. villosissimus* into the Simpson Desert is a rare event occurring, at most, every 20 years.

During the occurrence of *R. villosissimus* in the study area in 2010–2012 we observed three biotic interactions involving the species. The first was the apparent suppression of resident native rodents by the rats. This process was inferred both by changes in the population trajectories of native species following the appearance of *R. villosissimus* in 2010–2012 and by comparison of population trajectories during the 2010–2012 outbreak with those during the subsequent outbreak (2016–2017) when rats were absent. Responses were shown by *Notomys alexis* in sand environments and by *Pseudomys australis* at its refuge sites on cracking clay and gibber plains. *Rattus villosissimus* appeared to flatten the peak of the population outbreaks of these two species in 2010–2012 compared to 2016–2017.

The mechanisms by which *R. villosissimus* may have suppressed populations of other rodents potentially include predation (see below), interference competition and increased mortality resulting from stress. The mechanisms may differ between *P. australis* and *N.*



Fig. 5 Damage (indicated by arrows) sustained by a sapling *Acacia peuce* because of herbivory by *Rattus villosissimus*

alexis. With regard to interference competition, at refuges of *P. australis*, observations revealed that by May 2011 *R. villosissimus* occupied burrow systems that *P. australis* had continuously occupied since March 2009 (C. Pavey unpublished data). The fate of the previous occupants of the burrows is unknown. The role of stress on population regulation

Table 3 Mortality rate of tagged saplings of *Acacia peuce* in 14 monitoring plots from August 1983 to April 2019 both before and after the *Rattus villosissimus* outbreak of 2010–2012

Time period	No. deaths	Mortality/year	% survival	Source
Aug 1983-Feb 2011	40	1.45	72.7	Nano et al. 2012
March-December 2011	7	9.3	67.8	This study
Jan 2012-April 2019	3	0.41	65.8	This study

of mammals has been covered in detail from an intraspecific perspective by Sheriff et al. (2011). Less clarity is available on the role of interspecific interactions in producing stress. Given the high abundance of *R. villosissimus* in the study area in May 2011 and their close proximity to the resident rodents, it seems probable that the presence of rats would elevate levels of stress in other rodents.

An alternative explanation of the trapping results is that the presence of *R. villosissimus* and/or its odour in traps resulted in *P. australis* and *N. alexis* avoiding the traps such that the patterns observed do not represent an actual change in population trajectories of the two species. Such an avoidance response is widespread in mammalian prey species (Apfelbach et al. 2005; Fardell et al. 2020). In our study, *P. australis* and *N. alexis* may have been displaced and moved to adjacent areas that were not trapped or simply avoided the vicinity of traps at which odour indicated the presence of *R. villosissimus*. It is also possible that there was competition for traps in May 2011 with *P. australis* and *N. alexis* being inferior in competition for access to traps in comparison to *R. villosissimus* and *M. musculus*. Notably, the presence of *R. villosissimus* did not remove all *P. australis* from refuges as the two species continued to occupy these sites during sampling. Our data do not allow us to separate the two possibilities; either way the presence of the rats produced dramatic changes in the use of the landscape by two common resident, native rodent species.

The second novel interaction was the role of *R. villosissimus* as a predator. We noted predation by rats on *M. musculus* on multiple occasions including direct observations of rats hunting *M. musculus* at one of our camps and records of traps containing a *R. villosissimus* together with a partly consumed carcass of *M. musculus*. It is likely that *R. villosissimus* also preys on other rodents. We temporarily discontinued trapping in May 2011, for ethical reasons, after noting the predation of mice in traps by *R. villosissimus* based on the expectation that predation on other species in traps was inevitable. In arid South Australia *R. villosissimus* preys on *P. australis* during rodent outbreaks and it has long been recognised as partly carnivorous (Finlayson 1939; Bonyhardy 2019).

The third novel interaction was the consumption of foliage and bark of perennial vegetation. This interaction was noted on the long-term monitoring plots for saplings of the tree, *Acacia peuce*. All individuals in two of the 14 monitoring plots were damaged by *R. villosissimus* representing 32% of the monitored saplings. Of these 47 saplings, 10 subsequently died.

Herbivory by small mammals on perennial vegetation in semi-arid environments has been noted in South America (Farias et al. 2021) where it occurs after small mammal populations have rapidly increased in size, in response to productivity pulses of ephemeral vegetation, but then switch to alternative food sources during the intervening dry periods. Similarly, herbivory on *A. peuce* by *R. villosissimus* in our study was first detected towards

the conclusion of a prolonged period of high rainfall at a time when food resources for herbivores were declining (Nano and Pavey 2013). The population size of *R. villosissimus* was high at this time and, although *A. peuce* is patchily distributed, saplings provide a significant amount of bark and foliage across a drying landscape. This finding further supports the importance of *A. peuce* as a keystone species as its presence appears to have prolonged the rat outbreak in an otherwise treeless landscape.

Although previous research has reported herbivory by small mammals affecting growth and cover of perennial plants, *A. peuce* saplings in our study were killed by *R. villosissimus*. *Acacia peuce* is a rare and slow growing tree (Nano et al. 2012, 2013) and the mortality from *R. villosissimus* reported here is much greater than background rates of sapling mortality detected during monitoring of the plots since 1979 (Raghu et al. 2013). Therefore, the mortality caused by *R. villosissimus* is a potential concern for management of *A. peuce*. Although the impact is highly localised, the rat-driven mortality is of importance because of the small population size of *A. peuce* and the absence of other drivers of mortality. The *R. villosissimus* outbreak potentially also impacted early survival of seedlings; however, we did not collect data on this interaction. In future, seedling predation should be assessed using experimental exclosures that prevent the rats from gaining entry.

In addition to the novel interactions that we detail here, other ecological interactions can be triggered by irruptions of *R. villosissimus*. We have shown that rodent biomass was greater during the irruption with *R. villosissimus* than the following irruption without rats. Rats are consumed by a wide range of predatory vertebrates (Vernes et al. 2020; Pavey 2021) and an increase in rodent biomass provides increased food for predators with the possibility of trophic cascades generated by this increase. Our opportunistic observations also indicate that the digging activities of rats during the construction of burrows increased the movement of soil. The majority of digging mammals are extinct in the study area such that digging by *R. villosissimus* may be a positive process for ecosystem function because it bioturbates the soil contributing to a variety of biogeochemical processes that enhance aeration and water infiltration. This change can have positive impacts on ecosystem function through increased plant establishment and survival (James and Eldridge 2007).

In summary, outbreaks of *R. villosissimus* in the western Simpson Desert are rare events, more so than those of resident native rodents, occurring perhaps only every 30 years. When rats moved into the study area, a series of ecological interactions occurred that negatively affected the distribution and mortality of components of the ecosystem. Our study recorded potential displacement of native rodent populations, direct predation on rodents, and predation on bark and foliage of a keystone perennial tree. The ecosystem of the western Simpson Desert clearly has the ability to bounce back from these events. However, the ability to do so is likely to be related to the long return time of rat irruptions. If the intensification of the global hydrological cycle occurs as predicted by global climate models (e.g. Knapp et al. 2017), it will increase the occurrence of extreme precipitation years in arid Australia. This increase could result in an increase in occurrence of outbreaks of *R. villosissimus* in the western Simpson Desert. Such an increase may reduce the ability of the ecosystem to recover from the impacts of the rats. *Acacia peuce* and similar species will be at risk because of slow growth rates, rare reproductive events, and low levels of natural mortality.

Acknowledgements We thank Raquel, Peter, Colleen and Donny Costello for allowing us access to Andado Station. Access to the *Acacia peuce* at Akerre was granted by the traditional Aboriginal owners and we acknowledge them and thank the ranger groups at Aputula and Ltyentye Apurte for working with us to

monitor the trees. We thank John and Liz Spencer, Bob Stewart, and other caretakers for hospitality at Old Andado and Meegan Sullivan for facilitating our stays there. We are grateful for the field assistance provided by many dedicated people during this research. We appreciate the observational skills of Peter Nunn in noticing and bringing to our attention the impacts of the rats on *Acacia peuce*. Ethics approval was obtained from Charles Darwin University (number A07010) and CSIRO (numbers 2012-03, 2015-18, 2018-41) Animal Ethics Committees.

Author contributions C.P. and C.N. designed the study. C.P., S.R., G.K. and C.N. carried out the fieldwork. C.P. wrote the main manuscript text and prepared the figures. All authors reviewed and revised the manuscript.

Funding Open access funding provided by CSIRO Library Services. This work was supported by internal funding by the Northern Territory government and CSIRO.

Data availability The data that support the findings of this study are not openly available due to reasons of sensitivity and are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Apfelbach R, Blanchard CD, Blanchard RJ, Hayes RA, McGregor IS (2005) The effects of predator odors in mammalian prey species: A review of field and laboratory studies. Neurosci Biobehav Rev 29:1123–1144

Bonyhady T (2019) The enchantment of the long-haired rat: a rodent history of Australia. Text Publishing, Melbourne

Bowman TRS, McMillan BR, St. Clair SB (2017) Rodent herbivory differentially affects mortality rates of 14 native plant species with contrasting life history and growth form traits. Oecologia 185:465–473

Braithwaite RW, Griffiths AD (1996) The paradox of *Rattus tunneyi*: endangerment of a native pest. Wildl Res 23:1–21

Carstairs JL (1974) The distribution of *Rattus villosissimus* (Waite) during plague and non-plague years. Aust Wildl Res 1:95–106

Crombie AC (1944) Rat plagues in Western Queensland. Nature 3921:803–804

Dickman CR, Mahon PS, Masters P, Gibson DF (1999) Long-term dynamics of rodent populations in arid australia: the influence of rainfall. Wildl Res 26:389–403

Fardell LI, Pavey CR, Dickman CR (2020) Fear and stressing in predator-prey ecology: considering the twin stressors of predators and people on mammals. PeerJ 8:e9104. https://doi.org/10.7717/peerj.9104

Farias AA, Armias C, Gaxiola A, Cea AP, Cortes JL, López RP, Casanoves F, Holmgren M, Meserve PL, Gutiérrez JR, Kelt DA (2021) Species interactions across trophic levels mediate rainfall effects on dryland vegetation dynamics. Ecol Monogr 91:e01441

Finlayson HH (1939) On mammals from the lake Eyre basin. Part V Trans Royal Soc South Australia 63:348–353

Greenville AC, Wardle GM, Dickman CR (2013) Extreme rainfall events predict irruptions of rat plagues in central Australia. Austral Ecol 38:754–764

Greenville AC, Wardle GM, Nguyen V, Dickman CR (2016) Population dynamics of desert mammals: Similarities and contrasts within a multispecies assemblage. Ecosphere 7: e01343 (2016)

Hunt W, Birch C, Vanclay F (2012) Thwarting plague and pestilence in the Australian sugar industry: crop protection capacity and resilience built by agricultural extension. Crop Prot 37:71–80
James AI, Eldridge DJ (2007) Reintroduction of fossorial native mammals and potential impacts on ecosystem processes in an Australian desert landscape. Biol Conserv 138:351e359
Kechnebbou M, de Carvalho DL, da Silva PH, Silva DP (2021) Global warming drives range shifts in spiny-tailed lizards (Squamata: agamidae: *Uromastyx*) in the African and Arabian deserts. J Arid Environ 191:104522
Kelt DA (2011) Comparative ecology of desert small mammals: a selective review of the past 30 years. J Mammal 92:1158–1178
Knapp AK, Avolio ML, Beier C, Carroll CJW, Collins SL et al (2017) Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. Glob Change Biol 23:1774–1782
Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:1052–1055
Madsen T, Shine R (1999) Rainfall and rats: climatically-driven dynamics of a tropical rodent population. Austral Ecol 24:80–89
Madsen T, Ujvari B, Shine R, Buttemer W, Olsson M (2006) Size matters: extraordinary rodent abundance on an Australian tropical flood plain. Austral Ecol 31:361–365
McMahon TA, Murphy RE, Peel MC, Costelloe JF, Chiew FHS (2008) Understanding the surface hydrology of lake Eyre basin: part 1—Rainfall. J Arid Environ 72:1853–1868
Nano CEM, Pavey CR (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 Ecol 38:741–753
Nano CEM, Bowland AE, Nano TJ, Raghu S, Pavey CR (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. J Arid Environ 80:17–26
Nano CEM, Bowland AE, Nano TJ, Raghu S, Pavey CR (2013) Factors controlling regeneration in a rare desert tree *Acacia peuce*: limits to soil seed bank accumulation in time and space. J Arid Environ 90:114–122
Newsome AE, Corbett LK (1975) Outbreaks of rodents in semi-arid and arid Australia: causes, preventions and evolutionary considerations. In: Prakash I, Ghosh PK (eds) Rodents in desert environments, Junk, The Hague, pp 117–153
Pavey CR (2021) A nomadic avian predator displays flexibility in prey choice during episodic outbreaks of rodents in arid Australia. Oecologia 196:211–222
Pavey CR, Nano CEM (2013) Changes in richness and abundance of rodents and native predators in response to extreme rainfall in arid Australia. Austral Ecol 38:777–785
Pavey CR, Eldridge SR, Heywood M (2008) Native and introduced predator population dynamics and prey selection during a rodent outbreak in arid Australia. J Mammal 89:674–683
Pavey CR, Nano CEM, Cooper SJB, Cole JR, McDonald PJ (2011) Habitat use, population dynamics and species identification of mulgara, *Dasycercus Blythi* and *D. cristicauda*, in a zone of sympatry in central Australia. Aust J Zool 59:156–169
Pavey CR, Cole JR, McDonald PJ, Nano CEM (2014) Population dynamics and Spatial ecology of a declining desert rodent *Pseudomys australis*: the importance of refuges for persistence. J Mammal 95:615–625
Pavey CR, Addison J, Brandle R, Dickman CR, McDonald PJ, Moseby K, Young LI (2017) The role of refuges in the persistence of Australian dryland mammals. Biol Rev 92:647–668
Pavey CR, McDonald PJ, Cole JR, Nano CEM (2025) Site fidelity of the plains mouse, Pseudomys australis, in refuges during the transition from bust to boom. J Arid Environ 227:105296
Predavec M, Dickman CR (1994) Population dynamics and habitat use of the long-haired rat (*Rattus villosissimus*) in south-western Queensland. Wildl Res 21:1–10
Raghu S, Nano CEM, Pavey CR (2013) A demographic framework for the adaptive management of the endangered arid-zone tree species *Acacia peuce*. Aust J Bot 61:89–101
Redhead TD (1979) On the demography of *Rattus sordidus colletti* in monsoonal Australia. Australian J Ecol 4:115–136
Sheriff MJ, Dantzer B, Delehanty B, Palme R, Boonstra R (2011) Measuring stress in wildlife: techniques for quantifying glucocorticoids. Oecologia 166:869–887
Short J, O'Neill S, Richards JD (2018) Irruption and collapse of a population of pale field-rat at Heirisson prong, shark bay, Western Australia. Austral Ecol 40:36–46
Stringer EJ, Gruber B, Sarre SD, Wardle GM, Edwards SV, Dickman CR, Greenville AC, Duncan RP (2024) Boom-bust population dynamics drive rapid genetic change. PNAS 121:18e2320590121
Van Dyck SM, Strahan R (2008) The mammals of Australia, 3rd edn. Reed New Holland, Sydney

van Etten EJB (2009) Inter-annual rainfall variability of arid australia: greater than elsewhere? Australian Geogr 40:109–120

Vernes K, Elliott TF, Jackson SM (2020) 150 years of mammal extinction and invasion at Koonchera Dune in the lake Eyre basin of South Australia. Biol Invasions 23:593–610. https://doi.org/10.1007/s10530-020-02387-2

Wardle G, Pavey CR, Dickman CR (2013) Greening of arid australia: new insights from extreme years. Austral Ecol 38:731–740

White TCR (2019) The universal bottom-up limitation of animal populations by their food is illustrated by outbreaking species. Ecol Res 34:336–338

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.