Female reproductive suppression in an Australian arid zone rodent, the spinifex hopping mouse

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Abstract

The spinifex hopping mouse (*Notomys alexis*) is an Australian arid zone rodent that undergoes boom and bust population cycles in its natural environment. Most populations studied to date have been sympatric with exotic predators and introduced herbivores, likely affecting their population dynamics. Therefore, it is unclear whether high-density populations of hopping mice are regulated by purely extrinsic factors or whether intrinsic factors are also at play. We hypothesized that reproductive suppression of female *N. alexis* may occur in high-density populations as has been observed in some other rodent species. Reproductive condition of adult female *N. alexis* was compared between a high-density population within the Arid Recovery reserve, where exotic predators and introduced herbivores are excluded, and a low-density population on adjacent pastoral properties (no exclusions). Trap success was 10 times higher inside the reserve than at pastoral sites, and no adult females were observed breeding in the reserve population, despite 26 % of females at pastoral sites recorded breeding. Our results indicate that adult female *N. alexis* in the high-density reserve population were reproductively suppressed, but the similar sex ratios in both populations and the high female body mass and body condition in the reserve indicated that this was not due to demographic differences between the two populations or food scarcity. Our study indicates that the 'busts' observed in arid zone rodent populations may be amplified due to the presence of exotic predators and/or grazing by introduced herbivores. We contend that prior to the introduction of exotic predators and introduced herbivores in Australia, the arid zone rodent *N. alexis* would likely have been more abundant and intrinsic population regulation through female reproductive suppression may have played a larger role in population regulation.

Introduction

The spinifex hopping mouse (*Notomys alexis*) is an Australian arid zone conilurine rodent that undergoes 'boom and bust' population cycles in its natural environment (Masters, 1993; Predavec, 1994; Dickman *et al*., 1995, 1999; Southgate & Masters, 1996). Increases, or population 'booms', have consistently been correlated with extrinsic factors, mainly rainfall events in the preceding months (Masters, 1993; Predavec, 1994; Southgate & Masters, 1996; Dickman *et al*., 1999, 2010) and to some extent seed availability (Predavec, 1994). The cause(s) of population declines is more controversial. Some studies have suggested a link to scarce food resources (Predavec, 1994; Dickman *et al*., 1999) or predation by feral cats (*Felis catus*) and red foxes (*Vulpes vulpes*) (Newsome & Corbett, 1975; Dickman *et al*., 1999; Pavey, Eldridge &

Heywood, 2008; Moseby, Hill & Read, 2009; Letnic *et al*., 2011). Other studies have observed very few breeding females in high-density *N. alexis* populations, suggesting that reproductive suppression of females may occur in this species (Breed, 1976; Breed & Leigh, 2011; Breed, Leigh and Breed, 2017).

In some mammal populations, reproductive suppression inhibits population growth in high-density populations (Wolff, 1997). For instance, female reproductive suppression has been observed in high-density populations of northern hemisphere temperate zone cricetids and murid rodents including species of voles (Bujalska, 1973; Batzli, Getz & Hurley, 1977; Powell & Fried, 1992), deer mice (*Peromyscus*) (Terman, 1973) and house mice (*Mus musculus*) (Lamond, 1958; Drickamer, 1977). Female reproductive suppression may be a socially induced mechanism (Christian, 1971; Bennett, Faulkes & Molteno, 1996), rather than a response to dwindling food resources, and

it can reduce the chances of infanticide in species with aggressive or territorial females (Wolff, 1997). Species that have been observed to show female reproductive suppression tend to produce altricial non-mobile young, keep their young in burrows or dens and display female territoriality (Wolff, 1997).

Notomys alexis shares many characteristics with rodent species that have been observed to undergo female reproductive suppression. Individuals of this species live in mixed-gender groups in burrows where they raise their altricial young (Stanley, 1971; Happold, 1976). It is not known if females are territorial in the wild, but female *N. alexis* have been shown in laboratory trials to be significantly more aggressive to other females than are males (Stanley, 1971), suggesting that females could be territorial in their natural environment. However, field observations have noted that females held together in groups of up to five in temporary housing or captured in pitfall traps are not aggressive to one another (K. Moseby pers.obs). High population densities that deplete local resources are unlikely to persist under natural selection (Odum, 1971); therefore, it is plausible that Australian arid zone rodents could have evolved density-dependent self-regulatory mechanisms.

High-density populations of *N. alexis* are now mostly observed during resource pulses following rainfall (Letnic *et al.*, 2011), after which they undergo significant declines. However, rainfall alone does not always explain population responses (Bennison *et al.*, 2018), and the Anangu Aboriginal people of north-west South Australia reported that in the past, *N. alexis* populations could 'stay strong' even during droughts (Robinson *et al.*, 2000). Thus, the population crashes and subsequent low-density populations of *N. alexis* we now observe may be a consequence of predation by exotic predators and altered grazing regimes. In recent decades, exclosures have been established around Australia to exclude feral cats (*Felis catus*), red foxes (*Vulpes vulpes*) and grazing by introduced herbivores (Legge *et al.*, 2018). The Arid Recovery reserve is one of these projects (Moseby & Read, 2006) and supports high densities of *N. alexis*; up to 15 times higher than on adjacent pastoral grazing properties with exotic predators present, even during dry years (Moseby *et al.*, 2009; Read & Cunningham, 2010). Studies on *N. alexis* at this site have found higher rates of subadult captures outside than inside the reserve (Moseby *et al.*, 2009), suggesting that reproductive suppression may be occurring inside. This reserve provides an opportunity to investigate the population dynamics of *N. alexis* in an environment that may be more similar to the arid zone prior to European settlement and comparison with the adjacent lower-density population that occurs on adjacent pastoral properties.

The aim of this study was to investigate the factors that influence *N. alexis* population dynamics under high population density in the Arid Recovery reserve, where exotic predators and introduced herbivores have been excluded. We hypothesized that since *N. alexis* has some social and biological traits in common with northern hemisphere temperate zone rodents, reproductive suppression of female *N. alexis* may act to regulate high population densities in the absence of extrinsic factors.

Materials and methods

Site selection

Field work was conducted in South Australia within the Arid Recovery reserve (reserve) (30°29'S, 136°53'E) and at sites two and five kilometres from the western reserve fence boundary on adjacent pastoral properties (pastoral). The reserve is 123 km^2 in size and consists of six adjoining exclosures of which four (60 km^2) have had European rabbits (*Oryctolagus cuniculus*), feral cats and foxes eradicated for the purposes of reintroducing threatened mammal species (Moseby *et al.*, 2018). reserve trapping sites were established within the second expansion of the reserve, a feral free exclosure which also contained no reintroduced native species at the time of the study. This exclosure was chosen as it most resembled the outside areas in terms of species present (both with no reintroduced mammals). While the reserve fence excludes medium-sized mammals (Moseby & Read, 2006), small mammals such as rodents are able to move through the fence mesh. Thus the main difference between the sites was the presence/or absence of exotic predators and introduced herbivores.

Five sites were chosen within the reserve and five sites on the adjacent pastoral properties. We assumed that both reserve and pastoral sites sampled had been exposed to similar environmental conditions such as rainfall given their close proximity to one another. Sites within the same treatment group (reserve or pastoral) were situated at least 1.5 km from one another, so that discrete populations were likely to have been sampled. We did not record any marked individuals moving between sites during this study, supporting this assumption.

Reserve and pastoral sites were all situated on dunes dominated by wattle, *Acacia ligulata,* with some sticky hopbush, *Dodonaea viscosa,* present, as *N. alexis* tends to construct their burrows on dunes (Lee, Fleming & Happold, 1984). Gross habitat features were similar (i.e. longitudinal dunes with *Acacia* and *Dodonaea*) and treatments were in the same land-system, and sometimes on the same longitudinal dune, but microhabitat differences may have been present. All pastoral sites had evidence of cattle grazing at some time during the study (cattle directly observed at sites, or their dung and tracks observed) and rabbits and their scats were also observed. Feral cats and foxes were present outside the reserve, and their tracks were observed occasionally.

Trapping protocol

We conducted six trapping surveys at the 10 trap sites; five in 2005 (March, May, June, August and November) and one in 2006 (November). *Notomys alexis* were captured using aluminium box traps (Elliott traps) baited with a mixture of peanut butter and oats. Traps also had a wad of cotton wool placed inside to provide bedding during months of low overnight temperatures (May, June and August). Traps were placed well under vegetation to reduce exposure to the elements and reduce their visibility to Australian ravens (*Corvus coronoides*) which can interfere with exposed traps. Each trap site inside the reserve consisted of 10 traps spaced 10-15 m apart. Due to the low trap success at the

pastoral sites, these trap sites comprised 20 traps spaced 10–15 m apart. Traps were opened for 3–4 consecutive nights inside the reserve each trip, and simultaneously for 4–5 consecutive nights at pastoral sites. Traps were opened in the evenings and checked and closed at dawn each morning.

Trapped *N. alexis* were processed on site and then released immediately. Non-target species (*Pseudomys bolami, P. desertor* and *Mus musculus*) were captured infrequently and released immediately at the site of capture. All *N. alexis* captured were weighed and had their head and pes length measured to calculate a body condition score. Individuals weighing <20 g were classified as juveniles (Breed, 1983; Breed, 1989). To determine sexual maturity and/or reproductive activity, adult females had their vaginal appearance classified as either perforate, slightly perforate (with a pinhole-sized opening) or imperforate. Females with a fully perforate vagina were assumed to be sexually mature and/or reproductively active, and adult females with an imperforate or slightly perforate vagina were considered reproductively suppressed (Berris, Breed & Carthew, 2020). To assess whether females were currently breeding, the teats of adult females were examined to determine whether they were extended, and if they were then attempts were made to express milk to determine whether they were currently, or had recently been, lactating. If a female had extended teats, but was not lactating or obviously pregnant, it was assumed that suckling had taken place in recent months (Breed & Leigh, 2011; Breed *et al.*, 2017). Females suspected of being pregnant had their abdomen gently palpated to determine if intrauterine foetuses were present. All *N. alexis* were ear notched with a unique sequence (Wang, 2005) so they could be identified on subsequent trips. Animals recaptured more than once on the same trip were released immediately after the initial capture. Recaptures from previous trips had all measurements and reproductive activity assessments repeated to determine any changes over time.

The project methods were approved by the University of Adelaide Animal Ethics Committee (project numbers S-004-2005 and S-004-2005A).

Data analysis

Data were analysed using R version 3.3.1 (R Core Team, 2018). Mean values are given in the format mean ± SD. Overall trap success was estimated as the number of individuals captured per 100 trap nights over the entire survey for each treatment. Mean trap success and standard deviation for each survey were derived by grouping sites within treatments (reserve or pastoral) for each survey. Monthly rainfall data were obtained from the Bureau of Meteorology website for the weather station nearest to the trapping sites (Olympic Dam Aerodrome, Roxby Downs, approximately 10 km away) (http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=139&p_display_type=dataFile&p_startYear=&p_c=&p_stn_num=016096).

Body mass was compared between *N. alexis* at reserve and pastoral sites for all adults at the time of first capture (pooled across all surveys) using a t-test for females (data normally distributed, pregnant females excluded) and a Wilcoxon rank sum test for non-parametric data for males (data not normally distributed). Adult body mass was compared between surveys by using data on all adults (both recaptures and new captures) caught in each survey. Mean trap success and mean adult body mass were compared between surveys and treatments using a robust factorial two-way independent ANOVA with trimmed means (Wilcox, 2017) using the R package 'WRS2' with a 20% trimming level (Mair & Wilcox, 2019) due to small sample sizes and non-normal distribution of data.

Body condition was estimated for all adult *N. alexis* at the time of first capture, excluding pregnant females, using the scaled mass index (Peig & Green, 2009) which has been shown be a reliable measure of body condition in rodents and other small mammals compared with conventional condition index measures (Peig & Green, 2010). The scaled mass index was estimated for each individual from the following equation (Peig & Green, 2009):

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{\text{SMA}}}$$

where $\hat{M}_i$ gives the predicted body mass for an individual i when a linear body measurement (in this case head length) is standardized to L_0 (the mean head length for the study population). M_i and L_i are the body mass and head length, respectively, for an individual i, and b_{SMA} is a scaling exponent which is derived from the slope of a standardized major axis regression of the log-transformed weight and head lengths of all individuals. The predicted body mass at the mean head length ($\hat{M}_i$) for each individual gives a relative condition score for each individual. This scaled mass index was then compared between individuals from the two treatments (reserve and pastoral) using t-tests. Scaled mass index was estimated and compared separately for males and females.

Animals that had been ear notched and individually identified, but escaped before they could have their measurements taken at the time of first capture ($n = 7$) were used in calculation of trap success, but excluded from analysis that required body measurements at time of first capture. Head length was not recorded in November 2006; therefore, new captures on this trip were not included in the analysis of body condition.

Reproductive suppression and breeding were compared between reserve and pastoral sites by pooling all females captured in the two treatment groups, and then identifying how many of them were (1) observed with a perforate vagina at some stage during the study, (2) pregnant or lactating at some stage during the study, and (3) had extended teats during the study. The Pearson χ^2 test was used to test for an association between treatment (reserve or pastoral) and vaginal perforation and extended teats. The 'N-1' χ^2 test, which can handle expected frequencies below five (Campbell, 2007), was used to test for an association between treatment and lactating and/or pregnant females.

Results

Trap success

Trap success was around ten times higher at reserve sites than at pastoral sites over the study (Fig. 1). Inside the reserve,

there were 516 captures of 339 individual *N. alexis* (173 adult males, 164 adult females, two juveniles), yielding an overall trap success of 36.5 individuals per 100 trap nights. At pastoral sites, there were 118 captures of 85 individual *N. alexis* (48 adult males, 34 adult females and three juveniles), giving an overall trap success of 3.5 individuals per 100 trap nights. There was no significant difference in the sex ratio of adult *N. alexis* between the two treatments (Pearson $\chi^2 = 1.1$, d.f. = 1, $P = 0.30$). Mean trap success within each survey period was higher than overall trap success as it included marked individuals from previous surveys (Fig. 1). There was a significant effect of treatment (reserve or pastoral) on trap success (robust ANOVA with 20% trimmed means, $Q_a = 603.9$, $P = 0.001$). Trap success peaked at pastoral sites in November 2005, whereas at reserve sites the highest trap success was recorded in November 2006 (Fig. 1).

Body mass of adults

Mean adult body mass was significantly larger at reserve sites than at pastoral sites when pooled across all surveys for both female (Welch two-sample *t*-test, $t_{33} = -2.6$, P = 0.016) and male *N. alexis* (Wilcoxon rank sum test, W = 2041, $P < 0.001$) (Table 1). Mean adult body mass was also larger at reserve sites than pastoral sites in all surveys for males, and all surveys

except the August 2005 survey for females (Fig. 2). There was a significant effect of treatment (reserve or pastoral) on mean female body mass (robust ANOVA with 20% trimmed means, $Q_a = 11.2$, $P = 0.019$) and a significant interaction effect between treatment and survey on mean female body mass (robust ANOVA with 20% trimmed means, $Q_{ab} = 22.8$, $P = 0.04$). In adult males, there was a significant effect of treatment (robust ANOVA with 20% trimmed means, $Q_a = 48.3$, $P = 0.001$) and survey month (robust ANOVA with 20% trimmed means, $Q_b = 40.4$, $P = 0.001$) on mean body mass. There was also a significant interaction effect between the treatment and the survey month on mean body mass of male *N. alexis* (robust ANOVA with 20% trimmed means, $Q_{ab} = 28.3$, $P = 0.004$). Mean body mass at pastoral sites peaked during the August 2005 survey, following rainfall in June and July, for both males and females. Mean body mass then decreased again in the November 2005 survey (Fig. 2). Males at reserve sites followed a similar trend in body mass to adults at pastoral sites, albeit body mass in this cohort peaked slightly earlier in July 2005 (Fig. 2). However, females at reserve sites had a similar mean body mass in all surveys and body mass remained high in November 2005 (Fig. 2). The mean body mass of females was significantly larger than males at both reserve sites (Wilcoxon rank sum test, W = 18486, $P < 0.001$) and pastoral sites (*t*-test, t = 2.3, d.f. = 43.3, P = 0.027; Table 1).
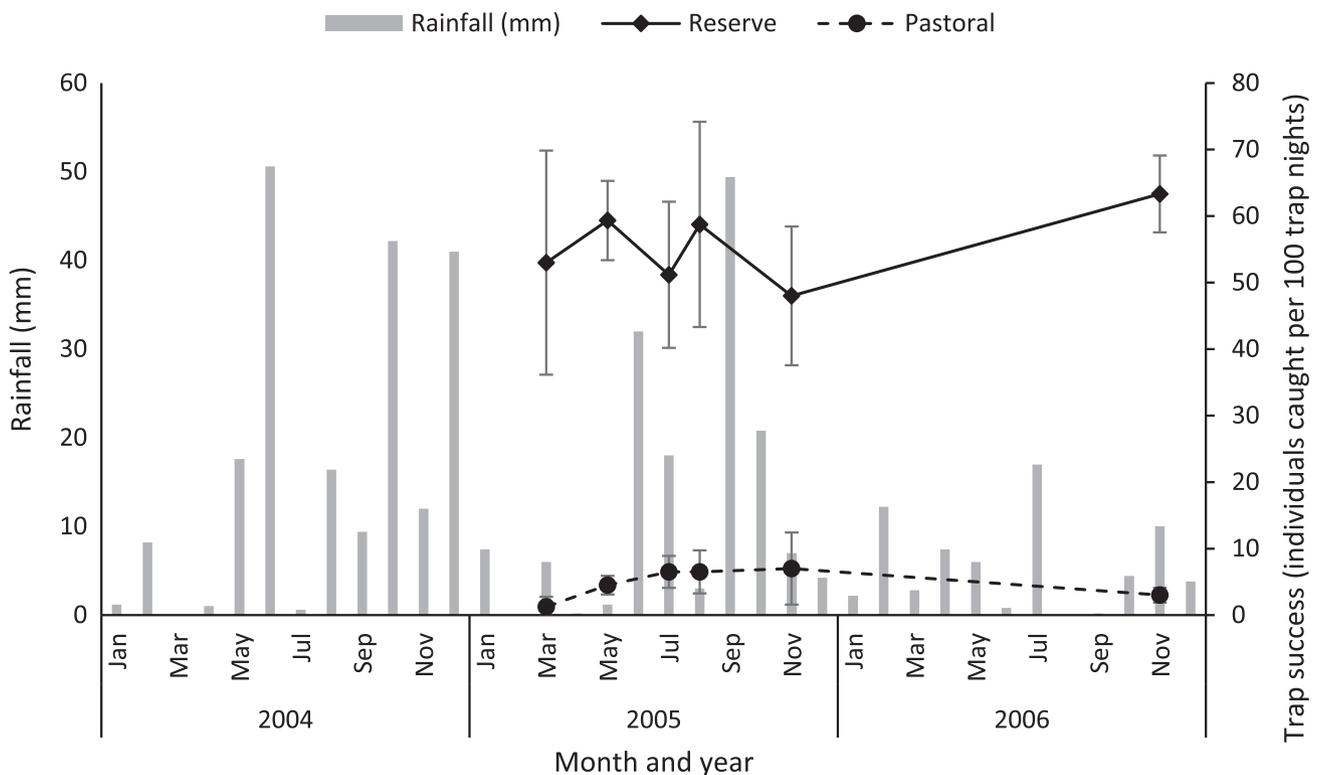

Figure 1 Mean trap success of *Notomys alexis* during each survey period recorded as the number of individuals trapped per 100 trap nights at sites within the Arid Recovery reserve and on adjacent pastoral properties (*n* = 5 sites in each treatment) with error bars representing the standard deviation. Rainfall (mm, grey bars) is recorded between 2004 and 2006 at the Olympic Dam Aerodrome, Roxby Downs, approximately 10 km from the site.

Body condition

Mean female body condition, as determined by using a scaled mass index, was significantly higher at reserve sites (37.4 ± 5.4 g, $n = 144$) than at pastoral sites (33.7 ± 7.5 g, $n = 23$) (Welch two-sample *t*-test, $t_{25.8} = -2.26$, $P = 0.03$). Mean male body condition was also significantly higher at reserve sites (34.2 ± 4.6 g, $n = 143$) compared with pastoral sites (30.5 ± 4.8 g, $n = 44$) (Welch two-sample *t*-test, $t_{69} = -4.58$, $P < 0.001$).

Breeding activity

A lower proportion of adult females had a perforate vagina, indicative of sexual maturation, at reserve sites in the high-density population than at pastoral sites (10 of 163 females in the reserve, 20 of 34 females at pastoral sites, Table 2). There was a significant association between treatment (reserve or pastoral) and vaginal perforation (Pearson $\chi^2 = 56.48$, d.f. = 1, $P < 0.001$) (Table 2). Of the 163 female hopping mice caught at reserve sites, 65 (40 %) of those were recaptured between 1 and 3 times after their initial capture. Four of these 65 females (6 %) initially had imperforate vaginae and were then observed to have developed vaginal perforation 3–5 months later when recaptured. All other (61) females were imperforate on all occasions they were captured. Eight adult females at reserve sites were trapped over a period of 12–20 months and were imperforate on all occasions. At pastoral sites, eight females were recaptured between 1 and 3 times following their initial capture. Six of these were imperforate at the time of their initial capture, four (67%) of which had become perforate when recaptured at a later date.

There was a significant association between treatment (reserve or pastoral) and breeding females (pregnant or lactating) (N-1 $\chi^2 = 44.98$, $P < 0.001$) (Table 2) with no breeding females observed in the reserve population. There was also a significant association between treatment and extended teats, indicative of previous recent suckling of young, (Pearson $\chi^2 = 21.49$, d.f. = 1, $P < 0.001$) (Table 2) with examination of the Pearson residual indicating a negative association between reserve sites and extended teats, and a positive association between pastoral sites and extended teats.

Timing of breeding and rainfall

In 2004, 200.2 mm of rainfall was recorded over a 12 month period prior to the start of the study. In 2005, there was 149.2 mm of rainfall, and in 2006 only 66.8 mm. The long-term average rainfall as given by the Bureau of Meteorology was 143.2 mm, thus rainfall was close to average in 2005 and considerably below average in 2006.

Females with a perforate vagina, indicative of sexual maturation and potential ovulation, were recorded in fewer surveys in the high-density reserve population than at pastoral sites (Fig. 3). Females with a perforate vagina were recorded at pastoral sites on all surveys except May 2005 (Fig. 3). Perforate females were only recorded inside the reserve in August and November 2005, following rainfall events between June and October 2005 (Fig. 3). No perforate females were caught inside the reserve in November 2006 following the year of low rainfall; however, two of the nine females trapped at pastoral sites were perforate (Fig. 3).

Evidence of breeding was recorded in the high-density reserve population on only two surveys. In November 2005, three months after perforate females were first observed in the reserve, juveniles (<20 g, $n = 2$) and females with extended teats (indicative of previous suckling, $n = 12$) were recorded in the reserve. One female with extended teats was also recorded at a reserve site in November 2006. By contrast, evidence of breeding was recorded in all surveys at pastoral sites. Lactating and pregnant females were recorded at pastoral sites in August 2005 (one lactating female and three pregnant females), November 2005 (one lactating female and three pregnant females) and November 2006 (one pregnant female). Juveniles were recorded in pastoral sites in March 2005 ($n = 1$) and November 2005 ($n = 2$). Non-breeding females with extended teats were recorded on all trips in the pastoral sites; however, the highest numbers were recorded in August 2005 ($n = 4$), November 2005 ($n = 6$) and November 2006 ($n = 3$).

Discussion

We found that the reserve population of *N. alexis* was larger but had lower breeding rates than the pastoral population, supporting observations by Moseby *et al.* (2009). The proportion of females with a perforate vagina at pastoral sites was almost 10 times the proportion found in reserve sites. Vaginal perforation correlates with sexual maturity and potential ovulation in laboratory colonies of *N. alexis* (Berris *et al.*, 2020) and imperforate females of adult body mass are in anoestrus (Breed & Leigh, 2011; Berris *et al.*, 2020). There was a high proportion of adult females with non-perforate vaginae in the high-density reserve population, despite suitable conditions for breeding at nearby pastoral sites. This suggests that oestrus had been inhibited and ovulation suppressed in these females within the

Table 1 A comparison of trap success and body mass of *Notomys alexis* within the Arid Recovery reserve and at pastoral sites

Site	Trap success (individuals/100 trap nights	Mean female body mass (pooled)	Mean male body mass (pooled)
Reserve	36.5	37.4 ± 5.4 g ($n = 163$)	34.4 ± 4.6 g ($n = 168$)
Pastoral	3.5	33.7 ± 7.4 g ($n = 29$)	30.1 ± 4.9 g ($n = 47$)

Overall trap success is given as the number of individuals caught over the entire study per 100 trap nights.
Mean female body mass and mean male body mass are based on body mass of adults recorded at the time of first capture and pooled across surveys.
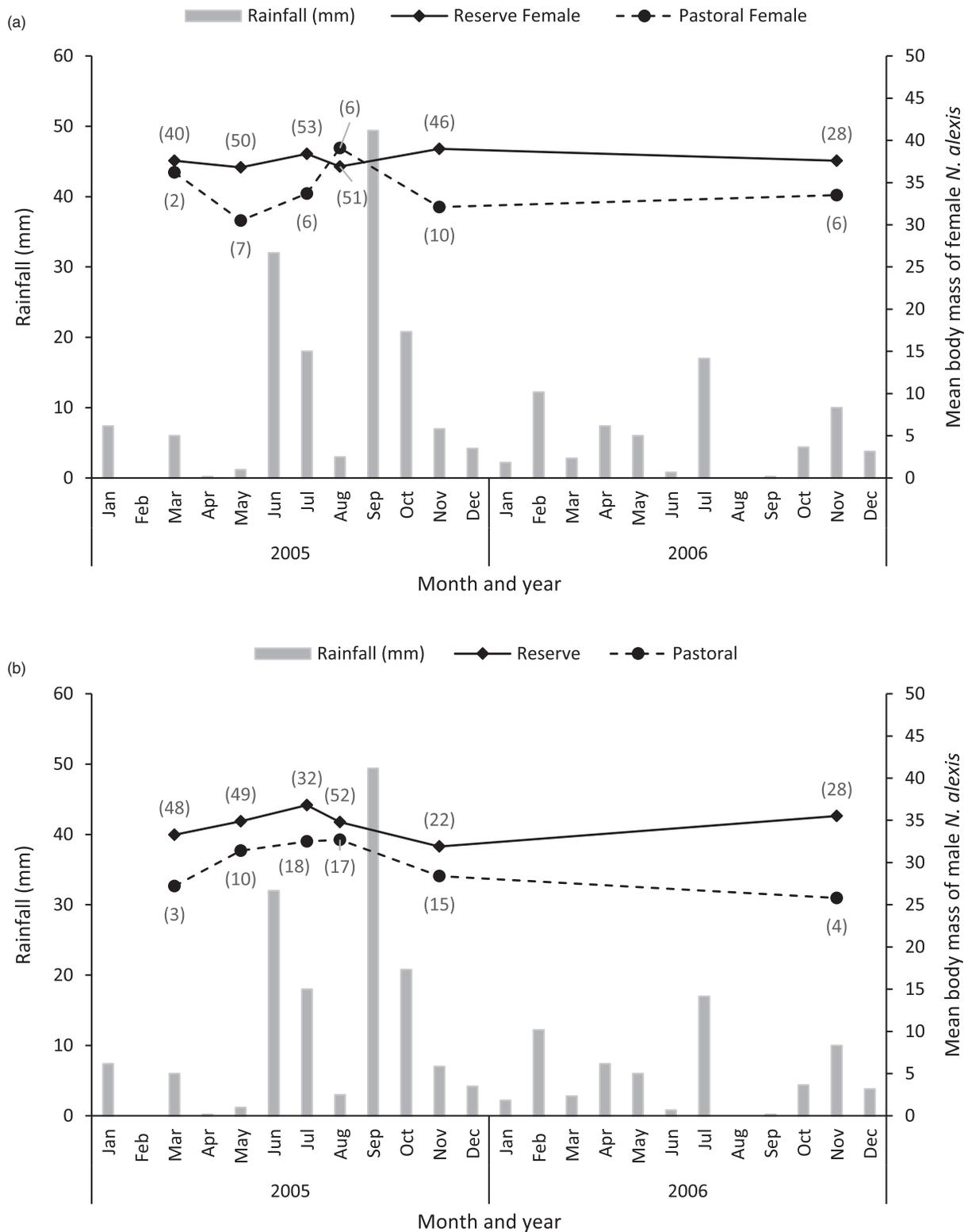Mean body mass is given in the format mean ± SD.

(a)

(b)

Figure 2 Mean body mass of (a) female *Notomys alexis* and (b) male *N. alexis* during each survey within the Arid Recovery reserve and at adjacent pastoral sites. Numbers in brackets represent the sample sizes for the corresponding data point. Rainfall (mm, grey bars) recorded during the study at the Olympic Dam Aerodrome, Roxby Downs, approximately 10 km from the site.

Table 2 Comparison of reproductive data of female *N. alexis* within the Arid Recovery reserve and at pastoral sites

Site	Trap success (individuals/100 trap nights)	Total number of adult females caught (*n*)	Reproductively mature (%)	Breeding females (%)	Females that had bred previously (%)	Number of juveniles observed (*n*)
Reserve	36.5	163	6 % (*n* = 10)	0 %	7% (*n* = 12)	2
Pastoral	3.5	34	59 % (*n* = 20)	26 % (n = 9)	38% (*n* = 13)	3

Reproductively mature females were those recorded with a perforate vagina, and breeding females were pregnant and/or lactating at some stage during the study.
Females that previously bred were those recorded with enlarged teats but from which milk could not be expressed.

reserve. Our results suggest there may be a link between high population density and female reproductive suppression in *N. alexis*. This supports previous studies that have observed few or no reproductively active females in high-density *N. alexis* populations during the height of 'boom' periods (Breed, 1976; Breed & Leigh, 2011; Breed *et al.*, 2017).

We failed to detect any pregnant or lactating females at reserve sites during the study. Furthermore, fewer juveniles and fewer adult females with extended teats, indicative of suckling in recent months, were observed in the reserve population. The two juvenile *N. alexis* trapped within the reserve indicates that some breeding may have occurred in this population, albeit at levels that were too low for us to detect breeding females. In contrast, breeding activity, including pregnant and lactating females, juveniles and/or females with extended teats, was recorded in each survey in pastoral sites. We also observed females within the reserve of large adult body mass (>40 g) remaining reproductively inactive over a period of almost 2 years. The results of our study therefore suggest that some adult female *N. alexis* living under high-density conditions for an extended time period may spend much of their life not breeding.

The mechanisms underlying lower breeding activity and reproductive suppression inside the high-density reserve population is unknown, but possible causes include differences in demography, rainfall and/or food resources between the two treatments, or reproductive suppression due to social mechanisms under high density. It is unlikely that in this case, the difference in breeding rates between the two treatments is due to demographic differences. In the laboratory, vaginal perforation can occur anytime from 40 days of age (Breed, 1975) in females with a minimum body mass of 24.2 g $\pm$ 3.0 g (Breed, 1989) and a pregnant female weighing 27 g has been recorded previously at the reserve (Moseby *et al.*, 2009). Females at reserve sites had a mean body mass of 37.4 g $\pm$ 5.4 g (*n* = 163), which was higher than females at outside pastoral sites and similar to the body mass observed in females at 24–36 months of age (Telfer & Breed, 1976). It is also unlikely that females were deprived of food resources at reserve sites. Both male and female *N. alexis* trapped within the reserve had a larger mean body mass and mean body condition than their counterparts at pastoral sites. These results indicate that *N. alexis* within the reserve were unlikely to be experiencing amplified nutritional stress under the high population density conditions compared to the individuals at pastoral sites. Although differences in rainfall between the two sites could

have driven site-based differences in breeding rates, sites were located within 5 km of each other and breeding differences were consistent over time.

In some northern hemisphere rodents, high population density and the resultant increase in social aggression and stress results in increased production of adrenocorticotropic hormone (ACTH) by the anterior pituitary, and resultant corticosteroids by the adrenal cortex (Christian, 1971). Increased concentrations of ACTH and adrenal corticosteroids inhibit sexual maturation and reproduction in female rodents (Christian, 1964) and may inhibit luteinizing hormone (LH) secretion (Christian, 1971). Therefore, in several northern hemisphere rodent species that show population fluctuations, the stress associated with a high population density has been causally linked to female reproductive suppression (Christian, 1971). Our study can neither support nor negate that a similar social mechanism is causing female reproductive suppression in *N. alexis*. In captive situations, familiar individuals have been observed to bond strongly with one another, however, the introduction of an unfamiliar individual results in much initial agonistic behaviour, particularly between females (Stanley, 1971). The limited studies on social organization on *N. alexis* suggest that burrow groups in the wild could be either stable (Stanley, 1971; Happold, 1976) or ephemeral in nature (Bradley, 2009), and that burrow groups are larger during times of high population density (Dickman *et al.*, 2010). As most behavioural research on *N. alexis* has been undertaken on captive colonies, it is difficult to determine which behaviours would occur naturally in the wild between individuals, and which are a consequence of living under captive conditions. Anecdotal information collected during 20 years of pitfall trapping at Arid Recovery suggests wild hopping mice are tolerant of each other when housed together in unfamiliar groups for short periods or when captured in large numbers in the same pitfall trap (K. Moseby, pers obs). Further research on sociality, behaviour and stress hormones in wild *N. alexis* populations is needed to determine whether social factors cause reproductive suppression in females.

Reproductive activity in both populations occurred shortly after rainfall was recorded in the area. Increased numbers of breeding females in the low-density population were recorded two to four months after significant rainfall events. Less breeding activity was recorded in November 2006 compared with November 2005 in both populations, which could be due to the lower total annual rainfall recorded in 2006. Population increases in arid zone rodents have been correlated with
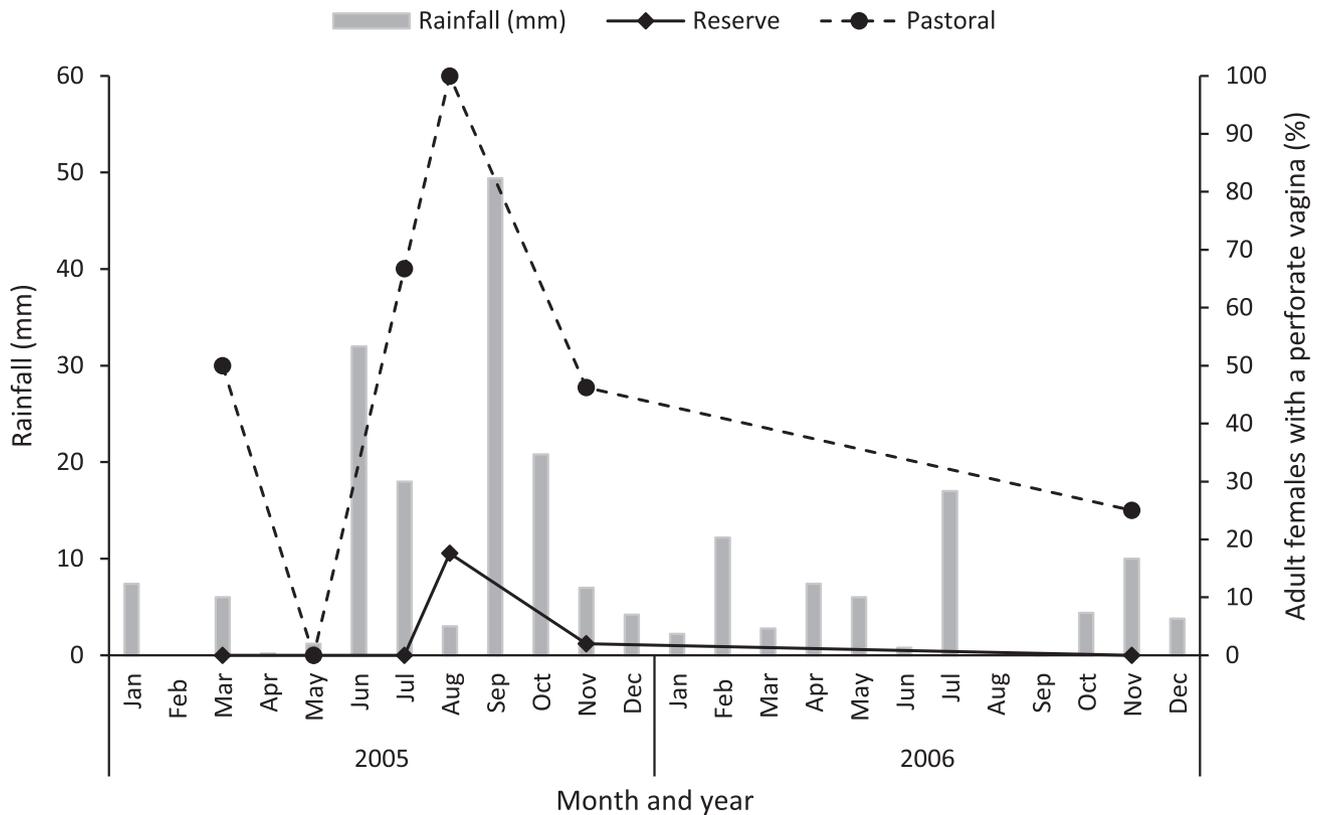
Figure 3 The percentage of adult females caught each survey with a perforate vagina at reserve and pastoral sites, and rainfall (mm, grey bars) recorded during the study at the Olympic Dam Aerodrome, Roxby Downs, approximately 10 km from the site.

rainfall in preceding months by numerous studies (Dickman *et al*., 1999, 2010; Pavey & Nano, 2013; Greenville *et al*., 2016). Our study demonstrates that increases in breeding activity can be observed approximately two months after significant rainfall events in *N. alexis*, which is consistent with increases in the population size observed in this species 3–10 months after large rainfall events in other studies (Dickman *et al*., 1999).

Our study consistently recorded higher trap success for *N. alexis* at reserve sites than at pastoral sites, supporting results from Moseby *et al*. (2009). The pastoral sites were also occupied by both introduced herbivores (European rabbits and cattle) and exotic predators (feral cats and red foxes). Predation by exotic predators has been shown to have significant negative impacts on Australian rodent populations (Davies *et al*., 2017; Murphy *et al*., 2019) and was thought to be the major reason for low hopping mice captures outside the reserve between 1998 and 2005 (Moseby *et al*., 2009). Small mammal and rodent captures have also been negatively correlated with both cattle grazing (Read & Cunningham, 2010) and vegetation cover reduction (Masters, Dickman & Crowther, 2003). Cattle grazing has been shown to impact on the survival, cover and recruitment of native arid zone plants (Read, 2004; Munro, Moseby & Read, 2009), as has grazing by rabbits (Lange & Graham, 1983; Munro *et al*., 2009), and reductions in rabbit

abundance has been correlated with increases in arid zone small mammal species (Pedler *et al*., 2016; Elsworth, Berman & Brennan, 2019). A reduction in vegetation cover through grazing may impact food resources for *N. alexis*, as well as increase the predation risk of rodents to exotic predators due to the removal of cover (Lawes *et al*., 2015). Therefore, the effects of introduced herbivores and predators are difficult to separate and are probably synergistic. The lower mean body mass, lower body condition and low trap success rates recorded at pastoral sites indicates conditions at pastoral sites were less favourable for *N. alexis* than at reserve sites. Our results suggest that *N. alexis* may have been much more abundant prior to the widespread occurrence of introduced herbivores and exotic predators, even during dry times, as reported by the Anangu Aboriginal people of north-west South Australia (Robinson *et al*., 2000).

Our study found adult female *N. alexis* had a significantly larger mean body mass than adult males in both populations. Sexual size dimorphism has been reported previously in captive colonies of *N. alexis* (Breed, 1983), and our results demonstrate this also occurs in wild populations. Most species in the order Rodentia tend to exhibit male-biased sexual size dimorphism, rather than female-biased as observed in *N. alexis* (Lindenfors, Gittleman & Jones, 2007). Larger females can occur due to selective pressures that favour larger females (e.g.

intense competition for resources; Ralls, 1976). However, another possible cause is reduced male–male competition in a species which then leads to smaller male body size (Isaac, 2005). Further research on the social organization of this species in the wild is needed to determine whether there are selective pressures acting on females that favour larger females.

Conclusion

Our results support the hypothesis that a high population density can result in female reproductive suppression in the Australian arid zone rodent *N. alexis*. The consistently higher capture rates and higher mean body mass of *N. alexis* within the reserve, where exotic predators and introduced herbivores were absent, suggests that the population 'busts' observed in arid zone rodent populations may be amplified by introduced threats. Prior to European settlement, *N. alexis* may have been more abundant and intrinsic population regulation mechanisms, such as female reproductive suppression, may have played a larger role in the population dynamics of this species.

Acknowledgements

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