

# Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal

K.E. Moseby<sup>a,b,\*</sup>, G.W. Lollback<sup>c</sup>, C.E. Lynch<sup>a</sup>

<sup>a</sup> Arid Recovery, P.O. Box 147, Roxby Downs, SA 5725, Australia

<sup>b</sup> University of New South Wales, Sydney, NSW 2052, Australia

<sup>c</sup> Design Unit, Engineering, Tweed Shire Council, Murwillumbah, NSW 2484, Australia

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## ABSTRACT

The failure of broadscale management to protect some threatened species has led to an increase in the use of islands and fenced reserves as translocation sites or foci for intensive threat mitigation. Although highly successful at excluding some threats, these sites may be prone to ecosystem imbalance due to the absence or removal of predators and competitors. We documented population trends and environmental impacts of the burrowing bettong, (*Bettongia lesueur*), a threatened herbivorous macropod reintroduced to a 1400 ha fenced reserve in arid Australia for 17 years after release. The population increased from 30 individuals to an estimated 1532 individuals (1.09 per ha), a density up to ten times higher than wild populations. There was little evidence that population growth was density dependent, the average intrinsic rate of increase ( $r$ ) was 0.125 and population size was unrelated to rainfall, body condition or reproductive output.

Browse damage on palatable plant species increased, and cover of palatable shrub species decreased, with increased abundance of bettongs. Activity of another reintroduced herbivore, the greater stick-nest rat, (*Leporillus conditor*), declined as bettong abundance increased while a reintroduced species not reliant on herbage was unaffected.

The burrowing bettong has been successfully reintroduced to the Arid Recovery fenced reserve but the positive average intrinsic rate of increase, inflated population density and impacts to resident plant and animal species suggests the population is now overabundant. This is the first documented case of overpopulation of a reintroduced species at a restricted site in Australia, highlighting the importance of preparing overpopulation management plans and considering reintroductions of species from all trophic levels including native predators.

## 1. Introduction

The number of threatened species continues to rise globally (IUCN, 2017) despite significant advances in conservation management. Methods used to protect threatened species and their habitat include invasive species management, habitat augmentation and population supplementation. In recent years, in situ broadscale management of threatened species has been supplemented by the reintroduction of threatened species to islands or fenced reserves (Long and Robley, 2004; Moseby and Read, 2006; Hayward and Kerley, 2009). Many government and private conservation organisations now rely on these relatively small and bounded areas for successful in situ protection or reintroduction of threatened species. Australia has > 32 fenced reserves larger than 10 ha (Dickman, 2012). Reserves usually protect populations from predation by cats (*Felis catus*) and foxes (*Vulpes vulpes*) and harbour threatened species such as the greater stick-nest rat (*Leporillus*

*conditor*) (Moseby and Bice, 2004), the eastern barred bandicoot (*Perameles gunnii*) (Arnold et al., 1990), western barred bandicoot (*Perameles bougainville*) (Richards and Short, 2003), burrowing bettong (*Bettongia lesueur*) (Short and Turner, 2000; Moseby et al., 2011) and bridled nail-tailed wallaby (*Onychogalea fraenata*, Hayward et al., 2014). In South Africa, fenced reserves play an important role in the preservation and reintroduction of the African elephant (*Loxodonta africana*) (Slotow et al., 2005) and black rhinoceros (*Diceros bicornis*) (Linklater and Swaisgood, 2008). New Zealand also has a network of fenced reserves protecting native species such as the little spotted kiwi (*Apteryx owenii*) from introduced predators including the stoat and weasel (Burns et al., 2011).

Islands and fenced reserves are often extremely effective at conserving specific fauna species due to their ability to exclude threats (Moseby et al., 2011). However, fenced reserves are costly to erect and maintain (Moseby and Read, 2006; Scofield et al., 2011). Furthermore,

\* Corresponding author at: Arid Recovery, P.O. Box 147, Roxby Downs, SA 5725, Australia.  
E-mail address: [k.moseby@unsw.edu.au](mailto:k.moseby@unsw.edu.au) (K.E. Moseby).

these sites may also be prone to ecosystem imbalance due to the removal of predators and/or competitors and the physical barriers to dispersal. These restricted sites are essentially closed systems that prevent the natural dispersion of enclosed animals (Slotow et al., 2005) and animals can increase in abundance relative to areas outside fences. In Africa, fenced reserves can lead to over-browsing of vegetation including *Acacias* by elephants (Hoare, 1992; Wiseman et al., 2004; Slotow et al., 2005) and vegetation damage has also been recorded in Australian fenced reserves by introduced native herbivores (Linley et al., 2016; Verdon et al., 2016). Unlike Africa where the carrying capacity of species within fenced reserves can be estimated by comparisons with unfenced populations (Hayward et al., 2007), in Australia there are very few areas where threatened mammal species remain in their natural state, thus rendering it difficult to ascertain natural population densities (Hayward et al., 2014). The absence of prior information on carrying capacity has led to informal debates over whether overpopulation actually exists in fenced reserves in Australia and when a population is considered overabundant.

Overpopulation of herbivores can be defined using a range of criteria including overgrazing. The definition of overgrazing varies according to the aims and outlook of the practitioner (Mysterud, 2006) but from a nature conservationist's perspective overgrazing can be defined as a time when grazing impacts are above a level at which other aspects of biodiversity are threatened (Mysterud, 2006). Overgrazing can lead to significant changes to vegetation (e.g. deer, Cote et al., 2004), causing major shifts in vegetation composition and ultimately stabilising at a level where there is a significant loss of productivity (Van de Koppel and Rietkerk, 2000). In addition to vegetation impacts, overgrazing can also negatively impact the abundance and community composition of a range of other fauna (for review see Foster et al., 2014). Sound conservation management suggests that herbivore abundance within fenced reserves should be managed to avoid impacts to other resident fauna and flora and to maintain ecosystem productivity.

Identifying overpopulation can be difficult in reintroduced populations as many translocated populations go through predictable post-release population changes including an initial establishment and high growth phase followed by a regulation phase where the population declines to carrying capacity and fluctuates in response to environmental conditions (e.g. Griffiths et al., 2017). Furthermore, any damage to vegetation needs to be considered in light of the ecosystem services that reintroduced species provide, including the provision of burrows for other fauna (Read et al., 2008), increased soil carbon and germination levels (James et al., 2010) and control of woody weeds (Noble et al., 2007). However, impacts of reintroduced species on in situ fauna and flora during the high post-release growth phase have the potential to reduce future carrying capacity and cause a legacy of impact that continues into the regulation phase. Despite the potential magnitude of impact, and calls for focussed research on the impacts of reintroduced species on their ecosystems (Armstrong and Seddon, 2008), very little attention has been given to the issue of overpopulation in the context of reintroductions.

Arid Recovery is an ecosystem restoration program located in northern South Australia and is based around a 123 km<sup>2</sup> feral-proof fenced reserve, the largest on mainland Australia. Feral cats, European rabbits (*Oryctolagus cuniculus*) and red foxes have been eradicated and excluded from 60 km<sup>2</sup> of this Reserve by a 1.8 m high feral-proof fence (Moseby and Read, 2006). Four locally extinct threatened mammal species have since been successfully reintroduced; the greater stick-nest rat, the burrowing bettong, the greater bilby (*Macrotis lagotis*) and the western barred bandicoot (*Perameles bougainville*). The burrowing bettong is a macropod and, due to the high population growth rates observed in related macropod species (Caughley et al., 1984), our study aimed to determine if the burrowing bettong has become overpopulated inside the Arid Recovery Reserve. In our study, we defined overpopulation as a population density higher than natural wild

populations, high population growth that was not strongly density dependent and induced measurable impacts on the survival, abundance or health of bettongs, flora or other resident fauna species. A previous study by Linley et al. (2017) recorded browsing on a range of plant species within the Arid Recovery Reserve close to bettong warrens but low sample size, an absence of data on long term trends in vegetation cover and relative abundance of bettongs meant that overpopulation could not be confirmed. We monitored long-term abundance, population growth, reproductive output and survival of bettongs as well as changes to the abundance of preferred dietary plant species, general vegetation cover and reintroduced native mammalian competitors. As the Arid Recovery Reserve is located in an arid environment where rainfall is low and erratic, we conducted our study over a long time period to avoid short term rainfall-induced changes in vegetation condition. The potential ecosystem benefits of the burrowing bettong reintroduction on soil, invertebrates or resident in situ fauna were not measured in this study but previous studies have found some ecosystem benefits do exist (Read et al., 2008; James et al., 2010). Long term management options for threatened species within fenced reserves are discussed.

## 2. Methods

### 2.1. Study area

The Arid Recovery Reserve is located 20 km north of Roxby Downs (30° 29'S, 136° 53'E) in the arid zone of northern South Australia (Fig. 1). The reserve is surrounded by a wire netting fence which

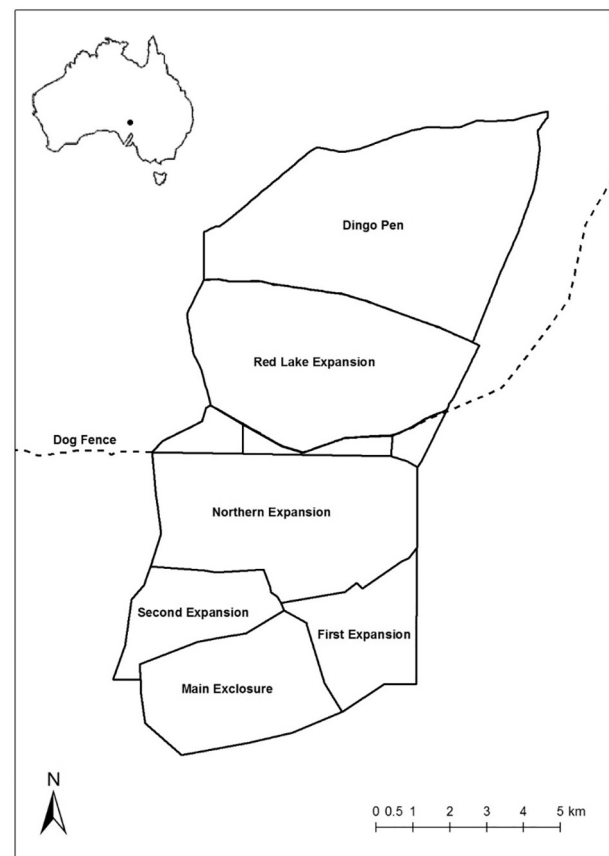
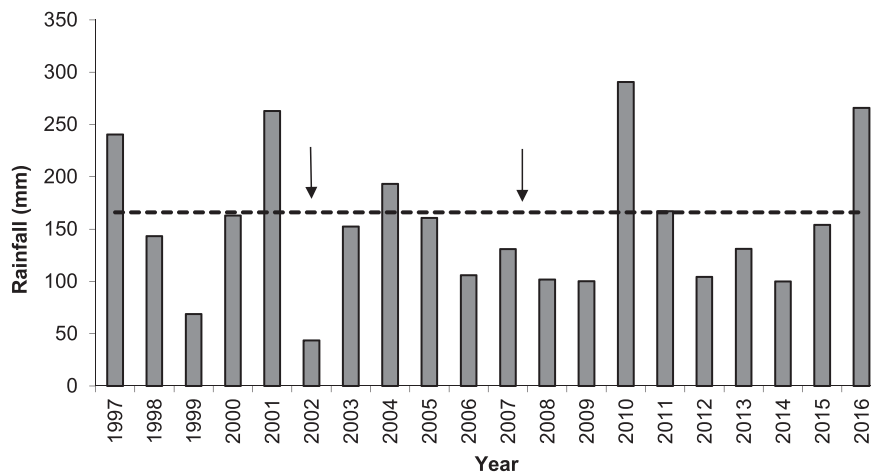


Fig. 1. Map of the Arid Recovery Reserve showing each paddock and the Dog Fence – an exclusion fence that keeps dingoes out of the area to the south of the fence. Burrowing bettongs were first reintroduced into the Main Enclosure and then into the First, Northern and Red Lake expansions. Bettongs naturally dispersed into the Second Expansion from the Northern Expansion by climbing over the short 900 mm high fence that separated the two areas. No bettongs are present in the Dingo Pen.

Fig. 2. Rainfall recorded at Arid Recovery between 1997 and 2016. Dotted line denotes the average long term annual rainfall. Arrows indicate drought events.



excludes cats, foxes, dingoes and rabbits (Moseby and Read, 2006). The Arid Recovery Reserve encompasses a range of arid zone habitats including longitudinal sand dunes dominated by sandhill wattle (*Acacia ligulata*) and sticky hop-bush (*Dodonaea viscosa*) interspersed with chenopod dominated clay swales (*Atriplex vesicaria* and *Maireana astrotricha*). Prior to the establishment of the reserve in 1997 the area supported conservative domestic stock grazing and herbivores such as red kangaroos, rabbits and native rodents. The reserve was considered to be in good condition when fenced due to the low density of permanent artificial water points for stock and the mixed age chenopod shrubland present (Read, 1992).

The average yearly rainfall for the Roxby Downs region is 166 mm but the average is not reached in 60% of years (Read, 1995). Rainfall in the region is sporadic and likely to fall in any month. During the study period from 1999 to 2017, above average rainfall was recorded in 5 years, average rainfall in 6 years and below average rainfall in 7 years (Fig. 2). There was no increasing or decreasing rainfall trend over the study period. We identified drought periods during our study as dry periods can lead to widespread decline or local extinction in some arid mammals (Masters, 1993; Brandle and Moseby, 1999; Moseby et al., 2006). Droughts were defined as severe rainfall deficiency periods of 12 months or more where the rainfall was among the lowest 5% on record (Australian Bureau of Meteorology, 2011). Rainfall data were used from the Olympic Dam Weather Station 10 km from the study site.

## 2.2. Study species

The burrowing bettong is a 1.6 kg endangered rat kangaroo within the family Potoroidae (Short and Turner, 2000). Burrowing bettongs are nocturnal and live communally in their own warren systems (Sander et al., 1997). At the time of European settlement, burrowing bettongs were widespread and abundant in arid and semi-arid Australia, with one of the most extensive ranges of any Australian marsupial (Finlayson, 1958). After becoming regarded as an agricultural pest (Finlayson, 1958), bettongs became extinct on the mainland due to intense competition from stock and rabbits and increased predation from introduced cats and foxes (Short and Turner, 2000; Short and Smith, 1994; Short and Turner, 1993). Although burrowing bettongs now only exist naturally on three islands off the coast of Western Australia - Bernier, Dorre and Barrow (Short and Turner, 1993) - populations have been reintroduced to the mainland in Western Australia, New South Wales and South Australia (e.g. Short and Turner, 2000; Moseby et al., 2011). Bettongs are primarily herbivorous browsers but will eat a variety of foods such as seeds, leaves, fruit, roots and occasionally invertebrates (Bice and Moseby, 2008).

## 2.3. Population trends

Burrowing bettongs were reintroduced to the Arid Recovery Reserve in September 1999 (10 individuals) and September 2000 (20 individuals) with animals sourced from Western Australia (Moseby et al., 2011). Bettongs were initially moved into the 14 km<sup>2</sup> Main Enclosure of the reserve which is surrounded by a 1.8 m high rabbit, fox and cat-proof netting fence. Low numbers of bettongs (< 30) were then gradually shifted to other fenced paddocks of the reserve where they naturally dispersed between some paddocks that were separated by lower 0.9 m high fences. After an initial 6 months of radiotracking individual bettongs, spoor transects and annual cage trapping were then used to monitor population trends in reintroduced mammal species.

Ten kilometres of spoor track transects were established in the Main Enclosure in 2000 and monitoring of them was undertaken between two and four times per year until 2016. For details of the method used see Moseby et al. (2009a, 2011). Bettong tracks per kilometre were averaged across the sampling periods in each year to give an annual track density and standard error. To determine if track counts were a robust technique for determining population size or density, we compared standardised track counts with population estimates derived from capture-mark-recapture-analysis.

Cage trapping for bettongs was undertaken on an annual basis in September from 2001 to 2011. A larger trapping event occurred in July and August 2013 and annual trapping resumed again in 2016. Between 2001 and 2010, trapping was undertaken at 84 trap sites in the Main Enclosure (Fig. 1), with one trap placed at each site and trapped for one night during each monitoring event. In 2013, bettongs were trapped over 1754 trap nights in the Main Enclosure to remove animals due to high population abundance. Traps were placed in a number of different locations throughout the Main Enclosure at varying trap effort but over the same sampling area (1400 ha Main Enclosure) as previous years. In 2011 and 2016 trapping occurred at the same 84 trap sites as 2001 to 2010 but traps were checked over multiple days to increase trap effort. The trapping region size (1400 ha) remained the same throughout the sampling years and was confined to the Main Enclosure, with only the effort differing between seasons. To account for changes in trap effort over time we included effort as a variable in the CMR models (see Analysis section below). Animals were captured using treadle-operated cage traps baited with rolled oats and peanut butter. All captured bettongs were marked with a unique eartag and released at point of capture.

## 2.4. Body and reproductive condition

The body and reproductive condition was recorded for all captured

animals during trapping events. Pouches were checked for the presence of pouch young and the proportion of females with pouch young was recorded during each trapping session. Body condition was recorded according to a categorical classification based on the amount of fat and muscle tissue felt between the spine and hip bones (excellent, good, fair, poor). The proportion of bettongs in the excellent or good condition classes was combined during each trapping event to account for any minor differences in scoring due to observer bias.

## 2.5. Impacts to local fauna and flora

To determine whether bettong abundance had a negative impact on local fauna and flora we measured activity of two other reintroduced fauna species (greater stick-nest rat and western barred bandicoot) and changes in the cover and/or damage to a range of palatable plants.

Greater stick-nest rats are a threatened herbivorous rodent that once occupied much of Australia's semi-arid zone (Copley, 1999). Rats were reintroduced to the Arid Recovery Reserve in 1998 and feed on succulent plants with a high water content. Their diet overlaps that of the burrowing bettong (Ryan et al., 2003; Bice and Moseby, 2008), so they were identified as species that could possibly be impacted by high bettong density. The stick-nest rat population was monitored using track counts (as per method above) and nest activity. Stick-nest rats build nests out of sticks and vegetation which can be as large as 2 m high and 3 m across. After the reintroduction of the stick-nest rat in 1998, active searches were conducted to locate 20 newly constructed nests for long term monitoring. Although other new nests were constructed over time, these initial nests were located in high quality habitat and trapping at these nest sites for 8 years revealed that female rats will take over unused nests if the previous occupants die or move away (K. Moseby unpublished data). Activity of these nests was monitored annually during 2001, 2003–2008, 2010 and 2013–2016. For each nest, active nests were identified by fresh stick-nest rat tracks and/or scats present and sometimes adults seen at the nest. The proportion of nests that were active was calculated for each annual monitoring event. Tracks of the reintroduced western barred bandicoots were also recorded annually from 2000 to 2016 and used as a comparison to stick-nest rat activity. This species is similar in size to stick-nest rats and was reintroduced to the reserve in 2001. They are omnivorous, feeding mainly on invertebrates and sometime seeds and as such are not considered as vulnerable as stick-nest rats to competition with burrowing bettongs.

Vegetation cover was recorded inside the Arid Recovery Reserve using step point transects conducted every 1 to 5 years over the study period, specifically during 2001–2004, 2006, 2010 and 2016. Between 500 and 600 step points were conducted at five dune sites inside the reserve and compared with five control sites outside the reserve where bettongs were absent. Herbivores present in the control area included rabbits and red kangaroos (*Macropus rufus*). Kangaroos were also present at low density within the Arid Recovery Reserve but at < 10% of outside densities (Arid Recovery unpublished data) and rabbits were absent from the reserve. Step point transects started 50 m each side of a site marker post with observers walking in the same direction looking at the horizon, only looking down to record the vegetation species or bare ground that was intersected by a mark on their boot on every second step. The percentage of total vegetation cover and combined cover of highly palatable shrubs were recorded during each monitoring session at inside and outside sites. Palatable plants were short-lived species recorded in the diet of burrowing bettongs at the reserve via faecal analysis (Bice and Moseby, 2008) and/or personal observation during nightly observations (pers obs). These included ruby saltbush (*Encalypta tomentosa*), *Salsola kali*, *Crotalaria eremaea* and *Atriplex velutina*. These plants have a high water content in their leaves, fruit and/or roots which are favoured by bettongs (Troughton, 1973) and other arid zone herbivores (e.g. Ryan et al., 2003) due to the limited availability of free water in the environment. Due to low patchy distribution

the cover of all palatable shrubs was combined for analysis. Ruby saltbush was also compared individually due to its known high palatability to bettongs (Bice and Moseby, 2008). To account for effects of rainfall, the proportional cover of each variable at inside compared with outside sites was also calculated.

One long-lived plant species with high moisture content was chosen for intensive monitoring to determine the impacts of browsing by bettongs. The native plum (*Santalum lanceolatum*) is a perennial shrub that is palatable to a range of herbivores such as domestic stock and rabbits (Chippendale, 1963; Ryan et al., 2003). The species grows approximately 2–3 m in height and occurs in small groves where it reproduces predominantly via suckering. Five native plum groves were sampled within the Main Enclosure of the reserve in April each year between 2000 and 2013 and in 2016, with no sampling occurring in the years 2006 and 2010. During each sampling event, up to 10 plants in each patch ( $n = 50$ ) were selected by random and assessed for browsing damage including bark stripping and branch breakage. For each plant, bark stripping and branch breakage were each scored between 0 and 4 based on; 0 = no browsing or bark stripping evident, 1 = minimal damage 1–10% of the individual plant affected, 2 = moderate damage 11–30% of the individual plant affected, 3 = high damage 31–75% of the individual plant affected and 4 = severe damage > 75% of the plant affected. Scores were summed for both bark stripping and branch breakage to generate a total score out of 8. The proportion of plants with high to severe damage (score  $\geq 6$ ) was recorded in each sampling session. Scats and tracks at the base of the shrubs were used to confirm that bettongs were the species responsible for the browse damage. The only mammalian browsers present in the reserve were bettongs and stick-nest rats, the latter never being observed browsing on native plum and no stick-nest rat scats were present at the base of plum shrubs.

## 2.6. Analysis

For annual cage trapping data, individual bettong captures were transformed into encounter histories and analysed to estimate abundance. The bettong population within the Main Enclosure was considered open because births and deaths occurred between sampling occasions. Hence, a Jolly-Seber model with a POPAN formulation (Schwarz and Arnason, 1996) was used to estimate annual survival ( $\phi$ ), capture probability ( $p$ ), Probability of Entrance ( $PENT$ ) and super-population size ( $N$ ). Derived abundance and recruitment at each occasion were also estimated. Models used a logit link function to estimate  $\phi$  and  $p$ , a multinomial logit link function to estimate  $PENT$  and a log link function to estimate  $N$ .

Goodness-of-fit was assessed on a global model – full group and time dependent  $\phi$ ,  $p$  and  $PENT$  – to test the assumptions that every marked animal at time ( $i$ ) has the same probability of capture ( $p_i$ ) and that every animal marked has the same probability of surviving regardless of when they were marked. Other models were constructed with either constant ( $\cdot$ ), time dependent ( $t$ ), sex dependent ( $s$ ) or an interaction between time and sex ( $t * s$ ) for the parameters  $\phi$ ,  $p$ ,  $PENT$  or  $N$ . Because trapping effort differed in some years, the number of trap nights in each monitoring session (effort) was used in some models to constrain  $p$ . Uneven intervals between trapping periods was accounted for in the analysis software, with parameters standardised to annual estimates. Models with poor estimates of survival or capture probability led to unreliable estimates of abundance and therefore were excluded from the suite of models. Model selection was assessed using a modified form of Akaike's Information Criterion (AICc) (Burnham and Anderson, 2002). The AICc formula includes a measure of fit and a penalty for model complexity and the lower the AICc value, the better the model is suited to the data. A suite of a priori models were analysed and therefore the difference between a particular model and the model with the lowest AICc was calculated ( $\Delta_i$ ). A  $\Delta_i < 2$  indicates substantial support for that model and a  $\Delta_i > 7$  suggests very little support for a particular model. From these differences, a relative weight of evidence for each model was



calculated ( $w_i$ ). POPAN model fitting, the goodness-of-fit test and the AICc calculation was performed in program MARK version 8 (White and Burnham, 1999).

A range of variables relating to bettongs and environmental variables were correlated against each other using a Spearman's rank correlation. Variables were considered highly correlated if  $P < 0.05$  and  $\rho \geq 0.70$ . The variables used in the correlation matrix were: bettong estimated abundance, bettong track density, bettong body condition, the proportion of bettong mothers that had active young in the pouch, yearly rainfall, one-year lag in yearly rainfall, stick-nest rat nest activity, stick-nest rat track density, the proportion of native plums with severe and high damage, ruby saltbush cover, combined palatable species cover, total vegetation cover and relative cover inside versus outside the Main Exclosure for ruby saltbush, palatable species and total cover. The variable "bettong estimated abundance" included both the capture mark recapture population estimates as well as the known abundance in 2000 when the species was reintroduced. Because sample size between variables sometimes differed, pairwise deletions of replicates occurred when samples were missing. Some highly correlated variables involved possible causal relationships and were investigated further using linear and non-linear least squares analysis. Plum damage and palatable plant cover were naturally a proportion and therefore were transformed using the following equation when used as response variable in a linear or non-linear analysis:

$$TY = \frac{Y_i}{1 - Y_i} + 0.001$$

where: TY = transformed plum damage or transformed palatable plant cover;  $Y_i$  = a replicate unit of plum damage or palatable plant cover. See Methods above for an explanation on the nature of the variable plum damage. Depending on the shape of raw data plots, linear, logarithmic, exponential, power and/or polynomial relationships were fitted and assessed using AICc. Correlations, linear analyses and non-linear analysis were undertaken using R 3.3.1 (R Core Team, 2016).

### 3. Results

#### 3.1. Population trends

Population trends were determined through spoor counts and capture-mark-recapture estimates. Thirty bettongs were released between 1999 and 2000 and the average number of bettong tracks per kilometre increased slowly for the first six years after release (Fig. 3). Track counts then generally increased rapidly from 2006 to 2016 with some

short declines in some years. Due to the rapidly increasing population, 132 were removed from the exclosure in 2008 and another 520 in 2013. Capture-mark-recapture data outlined in Section 3.1 below and presented in Fig. 4 indicate that these numbers represented 35% and 34% of the population at the time of removal respectively. Track counts temporarily declined slightly in the year after each removal event (Fig. 3) before increasing again the following year.

Annual cage trapping began two years after the first 10 bettongs were released in 1999 and one year after 20 were released in 2000. Trapping was conducted 13 times over the next 16 years. The number of trap nights per year was more or less even from 2001 to 2010 ( $\bar{X} = 78.3$ ,  $s.d. = 12.5$ ,  $n = 10$ ) and increased to 336 nights in 2011, 1754 nights in 2013 (due to the removal activity) and reduced to 336 nights in 2016. The number of bettongs caught was similar in most years ( $\bar{X} = 35.1$ ,  $s.d. = 9.6$ ,  $n = 9$ ), but was higher in 2008 (165), 2011 (195) and much higher in 2013 (527) and 2016 (416). The average male to female capture ratio was 1.23 to 1.

The overall goodness-of-fit test of the global model indicated that Cormack-Jolly-Seber mark-recapture assumptions were not violated ( $\chi^2 = 21.64$ ,  $df = 47$ ,  $P = 1.00$ ). A suite of 15 models were tested for the POPAN analysis, however, models with constant capture probability, varying capture probability with sex or effort are not listed because  $\Delta_i > 78$  for these models. Models where  $p$  was constrained to survey effort are not listed because  $\Delta_i > 45$  and models with constant  $N$  are not listed because  $\Delta_i > 94$ . Models would not converge when PENT did not vary over time. Models that included  $\phi(t)$  produced poor estimates of survival and were therefore not considered as competing models. Each model listed has pooled  $p$  for 2001–2003. The two models with the lowest QAICc values had varying  $\phi$  and  $N$  with sex and varying  $p$  and PENT over time (Table 1). These models are clearly best of the suite tested ( $w_i \sim 0.99$ ). There was little difference in these models and applying the principle of parsimony, it was decided to use abundance estimates from the model with the second lowest QAIC for abundance estimation and correlation analyses.

Estimated annual survival of the chosen model was 0.52 (SE = 0.02) for males and 0.56 (SE = 0.03) for females. The best model suggested that survival varied significantly between sexes but did not vary significantly over time. The probability of capture varied between 0.01 and 0.49. Derived estimates of abundance followed a similar pattern through time for both sexes because only  $\phi$  and (therefore)  $N$  differed between the sexes for the chosen model (Fig. 4). Abundance within the Main Exclosure steadily increased from 2001 to 2005 and then experienced larger increases punctuated with small decreases since 2007. Abundance estimates increased from 30 in 2000 to 1532 in

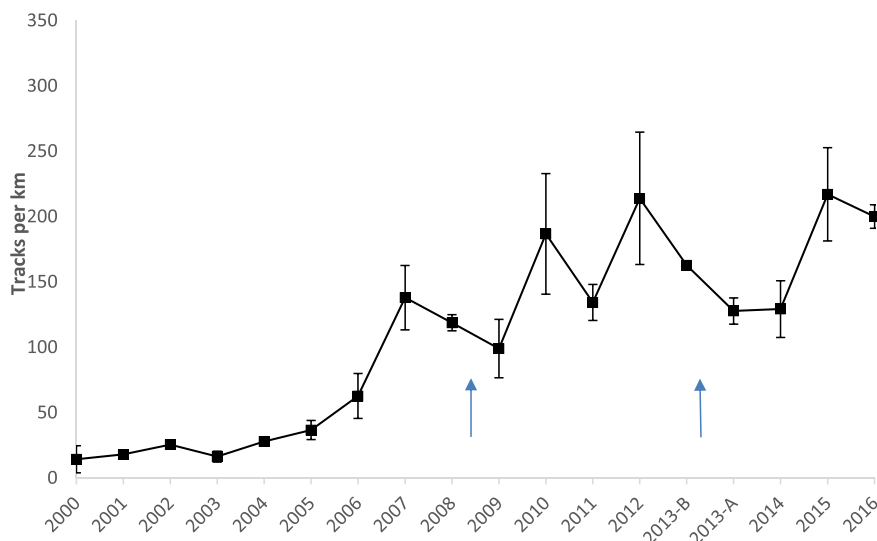
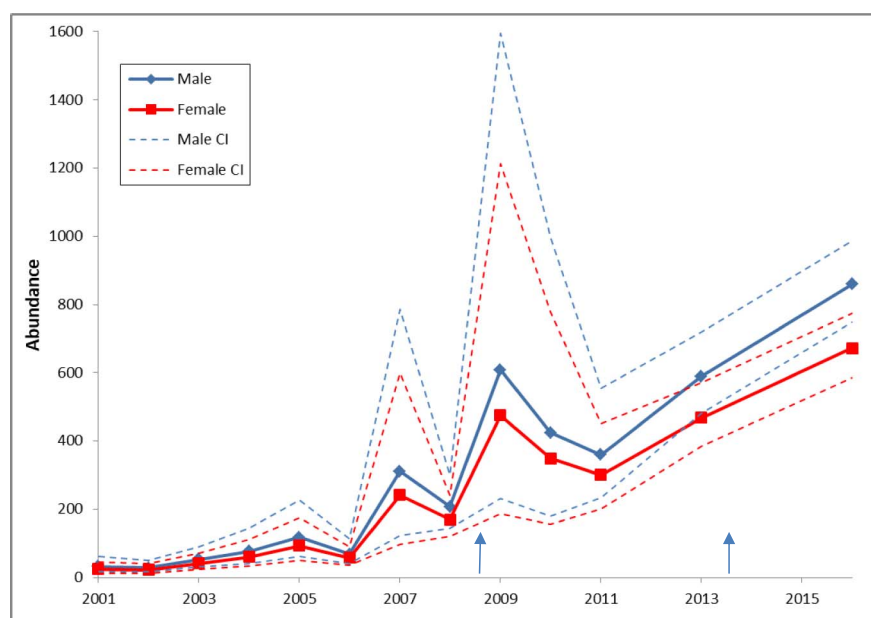


Fig. 3. Average annual bettong tracks per kilometre recorded along track transects within the Main Exclosure of Arid Recovery. Multiple counts were recorded within each year and so counts were averaged and bars denote one standard error. Arrows indicate when bettongs were removed from the exclosure, 132 bettongs were removed in 2008 and 520 in 2013. B refers to track count conducted prior to removal and A is after removal.



**Fig. 4.** Estimates of male (blue) and female (red) abundance and respective 95% CIs (dashed lines) derived from the chosen POPAN model. Arrows indicate when bettongs were removed from the enclosure. A total of 132 bettongs were removed in 2008 and 520 in 2013. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Performance of the better models analysed using the POPAN formulation to estimate survival ( $\phi$ ), probability of capture ( $p$ ), probability of Entry ( $PENT$ ) and super-population size ( $N$ ).  $t$  = time varying parameter;  $\cdot$  = constant parameter for sex and time;  $sex$  = parameter that varied between males and females;  $*$  = interaction between terms;  $\wedge$  = a model that had pooled  $p$  for 2001–2003 and also for 2013.

Model	K	AICc	$\Delta_i$ AICc	AICc $w_i$
$\phi(sex) p(t) PENT(t * sex) N(sex)^\wedge$	36	1803.57	0	0.63
$\phi(sex) p(t) PENT(t) N(sex)^\wedge$	27	1804.69	1.12	0.36
$\phi(sex) p(t) PENT(t) N(\cdot)^\wedge$	24	1812.78	9.21	0.01
$\phi(\cdot) p(t) PENT(t) N(sex)^\wedge$	25	1821.53	17.96	0.00

2016 (Fig. 4). The density of bettongs in the reserve in 2016 was 1.09 bettongs per hectare.

The 2009 estimate of abundance was left out of further analyses because of the large uncertainty in the estimate (Fig. 4). A power relationship best described the growth of abundance over time (Fig. 5). The next best fit was an exponential one ( $\Delta_i = 3.13$ ). The average annual percentage of growth of the bettong population from 2001 to 2016 was 52.7% and the average intrinsic rate of increase ( $r$ ) over the study period was 0.125 ranging from  $-0.22$  in 2006 to  $0.64$  in 2007. The two removal events in 2008 and 2013 occurred during the trapping session so the impact on population size was measured in the next trapping session after removal. There was no decline in bettong abundance in the trapping session after each removal of bettongs. There was no decline in estimated population size in the 2009 trapping event even when the wide confidence intervals were considered. There was no trapping event in 2014 or 2015 but the 2016 trapping event yielded the highest estimated abundance since the species was reintroduced. Droughts were recorded in 2002 and 2007/8. Although a slight decline in abundance was recorded in the first trapping session after the 2007/8 drought, confidence intervals suggest this was not significant (Figs. 2 and 4). There was no decline recorded after the 2002 drought.

### 3.2. Relationships between bettong and environmental variables

The correlation matrix revealed several highly significant relationships with  $\rho > 0.70$  (Table 2). There was a very strong association between bettong abundance and bettong track density and this relationship was best described with a power relationship, however, a

logarithmic relationship may also be suitable (Table 3, Fig. 5). The strong relationship between track density and bettong abundance suggested that the equation: Bettong abundance =  $0.227 * TD^{1.64}$ , where  $TD$  = bettong track density; may be used to estimate bettong abundance using track count data.

Both bettong abundance and track density were strongly correlated with two vegetation measures: plum damage and palatable plant cover. A linear model best described the relationship between bettong abundance and plum damage and while this was also the case for track density and plum damage, there was less certainty in deciding what shape best suited the latter relationship (Table 3, Fig. 5). Palatable plant cover declined and the severity of plum damage increased as bettong density increased (Fig. 5). A similar declining trend was seen in proportional palatable plant cover although a lack of replication and the use of proportional data likely prevented a significant correlation with bettong abundance. Proportion of palatable plant cover inside vs outside the Reserve dropped from near parity (0.98) during the first monitoring session in 2001 to 0.15 in the last session in 2016. In comparison, proportional total vegetation cover did not decline over the same period (0.9 in 2001 to 1.05 in 2016). A power model best described the relationship between transformed palatable plant cover and bettong abundance. While there was a clear negative relationship between the two variables, there is a fair amount of uncertainty regarding what was the best model likely due to few replicates of palatable plant cover (Table 3).

Body condition and proportion of females with pouch young were not correlated with bettong abundance. There were negative relationships between the proportion of females with pouch young and two variables: ruby saltbush cover inside the enclosure and relative ruby saltbush cover. Western barred bandicoot track counts were positively correlated with bettong abundance and this relationship is likely responsible for the negative correlation with palatable plant cover as the bandicoot is primarily insectivorous and not known to feed on the palatable species tested.

Although no significant correlation between bettong abundance and ruby saltbush cover was recorded, the average cover of ruby saltbush at dune sites inside the reserve declined from 1.4–2.65% of vegetation cover between 1999 and 2006 to 0.04–0.4% in 2010 and 2016. The influence of rainfall was isolated by comparing the proportion of ruby saltbush cover inside the reserve with outside sites. The proportion of

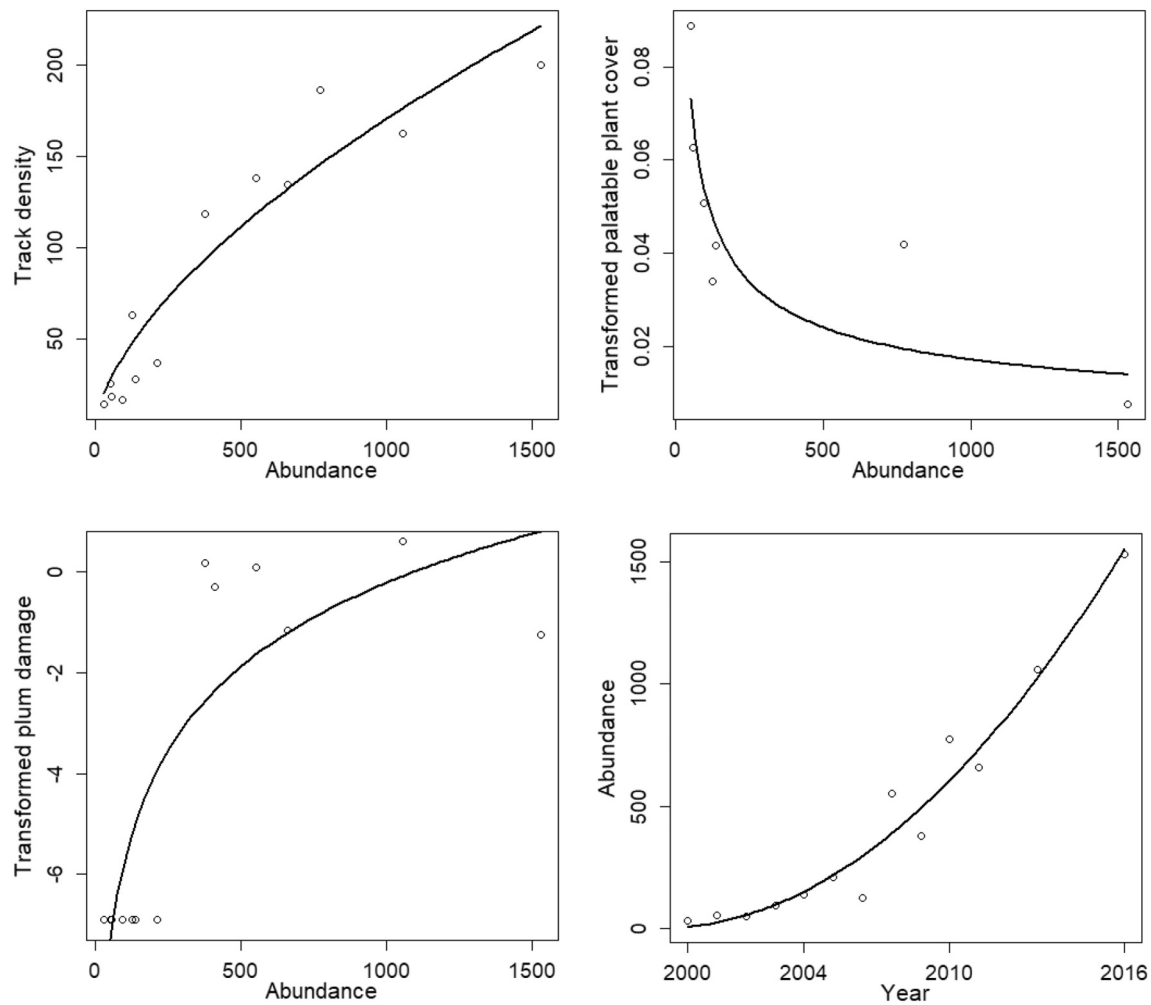


Fig. 5. Best model fit for various causal relationships using least squares. Top-left is a power relationship between bettong track density (tracks per km) and bettong abundance. Top-right is a power relationship between transformed palatable plant cover and abundance. See methodology for the transformation equation used. Bottom-left is a logarithmic relationship between transformed plum damage and bettong abundance. Bottom-right is a power relationship between bettong abundance and year. Abundance data does not include the 2009 estimate. See Table 3 for equations and model performance. Abundance data is included from capture mark recapture estimates (2001–2016) and known population size at time of reintroduction (2000).

ruby saltbush cover inside the reserve bordered on parity or increased relative to outside sites during the first 5 years after bettong reintroduction (0.95–1.32) before falling to 0.02 in the last monitoring session in 2016 (Fig. 6). The lack of significant correlation is likely influenced by the low number of sampling sessions in the last 10 years of the study as well as the increase in cover at inside sites initially followed by a sharp decline when bettong abundance reached high

levels.

Yearly rainfall and a one-year lag in yearly rainfall were not significantly positively correlated with any variable, except the proportion of active stick-nest rat nests, which was correlated with a one-year lag in rainfall ( $P = 0.02$ ,  $\rho = 0.74$ ). Stick-nest rat nest activity and track counts increased from 2002 to 2011 with a declining trend after 2011 (Fig. 7). Some of the large shrubs used as nest sites by rats were

Table 2

Rho values for highly correlated variables ( $\rho > 0.70$ ) that were significant at the  $P = 0.05$  level; \* = one-year lag in annual rainfall;  $n$  is shown in brackets; BA = bettong abundance; BTD = bettong track density; BC = bettong body condition; BAP = proportion of females with pouch young; WBBTD = western barred bandicoot track density; PLUM = proportion of native plums with severe and high damage inside the Main Exclosure; RSMO = a ratio of ruby saltbush cover measured inside the exclosure and outside the exclosure; SNRAN = proportion of active stick-nest rat nests; RS = ruby saltbush cover inside the Main Exclosure; TC = total vegetation cover inside the exclosure; TP = total cover of palatable plant species inside the exclosure. Variables that were not highly correlated with any other variables included stick-nest rat track density and relative cover inside versus outside the Main Exclosure for palatable species and total vegetation cover.

	Rainfall	Rainfall*	BA	BTB	BC	BAP	WBBTD	PLUM	RSMO
BTB			0.95 (13)						
SNRAN		0.76 (10)							
WBBTD			0.91 (13)	0.85 (15)					
PLUM			0.79 (12)	0.84 (14)					
RS	−0.89 (7)					−0.90 (7)			
RSMO						−0.70 (8)		−0.76 (7)	
TP			−0.86 (7)	−0.80 (7)			−0.86 (7)		
TC					0.79 (7)				0.79 (7)

**Table 3**

Linear and non-linear model performance for causal variables that were highly correlated. Polynomial relationships were 2nd order. TD = bettong track density; A = bettong abundance; PD = plum damage, TPD = transformed plum damage, TPPC = transformed palatable plant cover. See [Methods](#) for transformation details.

Model type	AICc	$\Delta_i$ AICc	AICc $w_i$	Formula
Bettong track density vs. bettong abundance				
Power	42.54	0	0.61	TD = $2.47 \times A^{0.61}$
Logarithmic	44.04	1.58	0.28	
Linear	45.81	3.35	0.11	
Plum damage vs. bettong abundance				
Logarithmic	12.21	0	0.83	TPD = $5.524 \times \log_{10}(A) - 16.786$
Linear	15.45	3.23	0.17	
Plum damage vs. track density				
Linear	13.02	0	0.45	TPD = $-0.075 + 0.004 \times TD$
Logarithmic	13.26	0.25	0.40	
Polynomial	15.19	2.18	0.15	
Palatable plant cover vs. bettong abundance				
Power	-12.80	0	0.38	TPPC = $0.49 \times A^{-0.49}$
Logarithmic	-12.07	0.72	0.27	
Linear	-11.28	1.51	0.18	
Exponential	-11.25	1.54	0.18	
Palatable plant cover vs. bettong track density				
Logarithmic	-18.81	0	0.26	TPPC = $-0.04 \times \log_{10}(TD) + 0.11$
Exponential	-18.80	0.01	0.25	
Linear	-18.73	0.08	0.25	
Power	-18.71	0.10	0.24	

impacted by bettongs during the study period through browsing or root damage, occasionally resulting in plant death (see [Plate 1](#)).

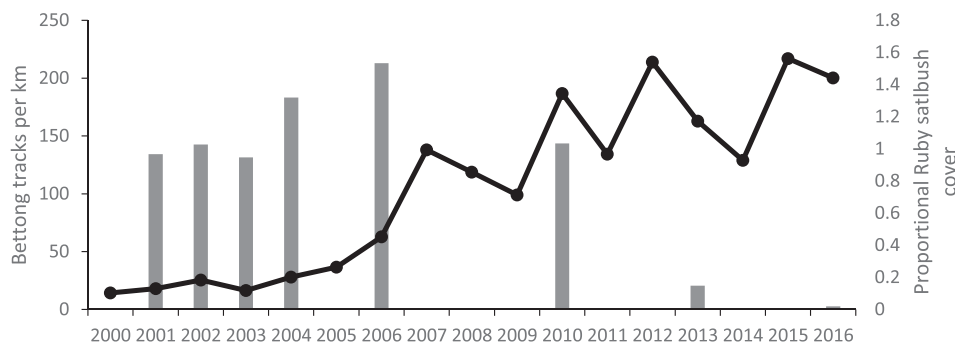
#### 4. Discussion

Burrowing bettong abundance increased significantly from 30 to 1500 individuals during the 17 years after release into the fenced Arid Recovery Reserve. This increase represented a power growth rate indicating that growth was a decreasing function of density. Power growth rates are common in territorial mammals ([Tanner, 1966](#)) with competition between conspecifics for territories eventually limiting growth rates. However, several factors suggest bettong population growth is not strongly density dependent. The power growth rate result may have been influenced by the removal of one third of the bettong population at two periods during the study and without this removal, a faster exponential growth rate may have been recorded. This is supported by the result that bettong survival, body condition and reproductive output were not correlated with time since release or bettong abundance. Additionally, the close fit of both power and exponential growth rates suggests there is no clear density dependence.

The average intrinsic rate of increase ( $r$ ) of bettongs was 0.125 which reached levels as high as 0.64. In comparison, most animal populations fluctuate from year to year but have an average rate of increase of 0 ([Caughley, 1980](#)). The highest annual rate of increase we

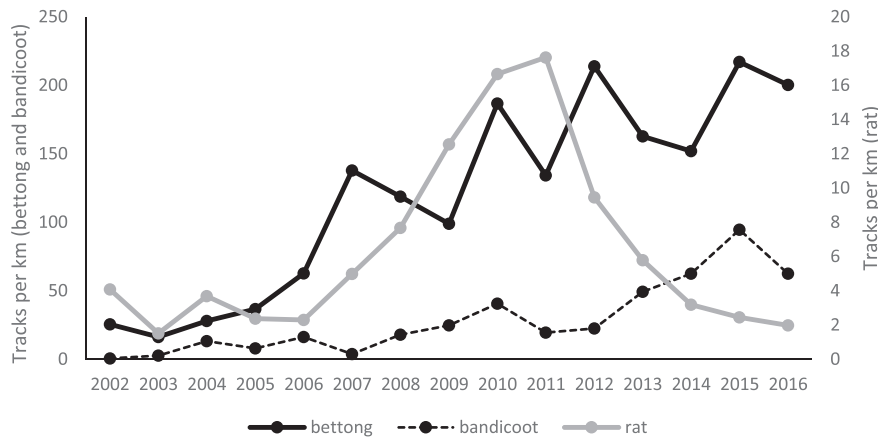
recorded in the burrowing bettong is similar to that recorded in certain years by other arid macropods such as the red kangaroo which can increase at a rate of 0.45 ([Caughley et al., 1984](#)) and 0.67 per annum ([Poppe and Grigg, 1999](#)) after rain. This growth rate is higher than other macropods in mesic areas and is thought to be an adaptation to unpredictable rainfall in desert regions. Like other macropods, wild burrowing bettong populations on offshore islands also experience fluctuations in relation to rainfall ([Short et al., 1997](#); [Short and Turner, 1999](#)). However, burrowing bettong abundance at Arid Recovery was not influenced by rainfall or drought and the density of burrowing bettongs at Arid Recovery was 1.09 per hectare in 2016; nearly 10 times higher than the density reported on two of the three remaining wild populations of bettongs on more productive islands (250 mm rain vs 160 mm rain per year) during dry years (0.14–0.17 per ha, [Short and Turner, 1993](#)) and 2.5 times higher than reported in average or above average rainfall years (0.44 per ha, [Short et al., 1997](#)). Bettong density at Arid Recovery is also 10 times higher than the population density of the third wild population present on Barrow Island (0.17, [Richards, 2007](#); 0.15, [Richards, 2012](#)) which has a mean annual rainfall (320 mm) twice that of Arid Recovery. These differences may be at least partly due to the fact that bettongs were reintroduced to unoccupied habitat in our study and are still within the establishment phase where high population growth can exceed carrying capacity. Additionally, the wild sites also support sympatric macropod species ([Short et al., 1997](#)) which may reduce the density of individual species but not necessarily lead to lower total grazing pressure than recorded at Arid Recovery. Although these similar-sized native herbivores may compete with bettongs and reduce bettong density, Arid Recovery also supports other native herbivores including sleep lizards, stick-nest rats and small native rodents ([Moseby et al., 2009b](#)) which may also compete with bettongs for food.

Although the current high growth rate and inflated density relative to wild populations may eventually be limited by competition or resources, significant damage to palatable plant species is already occurring with likely flow on effects to other resident species. Bettong abundance was significantly correlated with native plum damage and a decline in palatable shrub cover. In particular, the initial increase in ruby saltbush cover inside the reserve relative to outside has now been reversed. A decline in abundance of, and an increase in browsing damage to, ruby saltbush within the reserve has been attributed to burrowing bettongs in earlier studies at Arid Recovery ([Gerlach, 2006](#); [Linley et al., 2016](#)) and seedlings of ruby saltbush are less abundant at other reintroduction sites where bettongs are present ([Verdon et al., 2016](#)). Native plum and ruby saltbush are highly palatable ([Bice and Moseby, 2008](#)), have high water content and ruby saltbush in particular is utilised by a range of bird ([Tester et al., 1987](#)), mammal ([Ryan et al., 2003](#)) and reptile species ([Dubas and Bull, 1991](#)). These fleshy-fruited plants with high water content are uncommon in arid areas ([Willson et al., 1989](#)) and are likely to provide important food during drought conditions. The absence of a correlation between bettong abundance and total vegetation cover suggests that either many species are not



**Fig. 6.** Bettong abundance (black line indicates tracks per km) over the study period on the main axis and bar graph showing proportional cover of ruby saltbush inside vs outside the reserve on the secondary axis. When cover is equal inside and outside the reserve then proportional cover is 1. Ruby saltbush cover was not measured in 2005, 2007–2009, 2011–2012 and 2014–2015. The proportion of ruby saltbush in 2016 was 0.019.





**Fig. 7.** Track counts of bettongs and two other reintroduced species that are similar to each other in size (western barred bandicoots and stick-nest rats) from 2002 (first time that all three species were monitored simultaneously) to 2016. Stick-nest rat tracks are presented on the second axis.



**Plate 1.** Stick nest rat nest within *Sarcostemma* spp. (top left), nest abandoned after plant was killed by bettongs (top right), plant being destroyed by bettongs (bottom left).

palatable or that browsing damage does not yet extend to less palatable plant species. Other studies have shown that confining herbivores to fenced areas can cause increases in their population size, and restrict their movement and dispersal (Slotow et al., 2005; de Torres and Marlow, 2012; Hayward and Somers, 2012), leading to vegetation change (Cassidy et al., 2013). Severe browsing damage by elephants and other African species has been recorded within fenced reserves (Hoare, 1992; Boone and Hobbs, 2004; Wiseman et al., 2004) and significant vegetation changes have been recorded in areas of Australia when macropod populations have increased to high levels (Dexter et al., 2013; Linley et al. 2016).

Although a significant correlation with bettong abundance was not recorded, spoor counts suggest that the reintroduced stick-nest rat may

have also declined within the reserve since the increase in bettong population and bettongs have been observed destroying bushes that shelter rat nests and heavily grazing palatable plants near nest sites. The impact of bettongs on the stick-nest rat is supported by the fact that the western barred bandicoot, a similar-sized reintroduced species that is not reliant on browse, did not decline over the same period. Overgrazing by other macropod species has been shown to impact a range of taxa including reptiles (Manning et al., 2013; Howland et al., 2014) and other threatened mammals (Winnard and Coulson, 2008). Further detailed study of the stick-nest rats at Arid Recovery including exclusion experiments is needed to confirm and quantify the impact of bettongs on this threatened species.

The positive average intrinsic rate of increase, excessive population

size compared with wild populations and damage to in situ plant species suggests that the burrowing bettong is now overabundant within the Arid Recovery Reserve. The lack of a significant correlation between bettong abundance and variables such as breeding, body condition or rainfall suggests that neither extrinsic nor intrinsic factors are currently limiting the population and it is still within the post-release growth phase, 17 years after release. A contributing factor to the high bettong abundance at Arid Recovery and species within other fenced reserves is the absence of top down pressure from predation. The burrowing bettong has no natural predators within the reserve except for diurnal wedge-tailed eagles that predate upon bettongs if they emerge during the day; an event that has only been occasionally observed over the 17 years post-release (pers. obs.) and usually during prolonged dry conditions. The dingo (*Canis lupus dingo*) is an important predator of macropods and quoll (*Dasyurus* spp.) species will consume some small macropod species but the dingo has now been excluded from southern Australia by the Dog Fence and quolls became extinct in the arid zone after European settlement (Woinarski et al., 2012). In areas where predators have been removed, macropod densities have significantly increased (Caughley et al., 1997; Dexter et al., 2013). Macropod overpopulation is a widespread issue in Australia with many government departments and organisations implementing control programs in areas where predators of macropods are no longer present. Overpopulation of herbivores is also a concern in other countries and on islands where predators have been controlled or removed (Kunovac, 2001). For example, rabbit populations increased significantly and caused severe vegetation damage on Macquarie Island in the years following feral cat eradication (Bergstrom et al., 2009).

Animal populations eventually become limited by intraspecific competition, resources or predation, and ultimately reach their carrying capacity. In the absence of natural predators, it is likely that the bettong population will eventually become limited by competition or food resources and eventually reach the regulation phase where it will stabilise at a lower density and become density dependent. Fencing parcels of land into fragments can reduce carrying capacity by restricting the movement of herbivores and reducing their access to high quality habitat patches (Boone and Hobbs, 2004). Although at some point carrying capacity will be reached and the abundance of herbivores will stabilise or decline, overgrazing can occur before populations reach carrying capacity, thus leading to permanent and irreversible changes to the ecosystem (Myserud, 2006). Conservation ethics suggests that intervening before this occurs is sound management practice, particularly in confined areas where native predators are excluded and natural dispersal cannot occur.

Strategies to control overpopulation of animals can include forced or assisted removal of animals (Crisp and Moseby, 2010; Bannister et al., 2016), culling (Clarke and Grey, 2010; de Tores and Marlow, 2012) and sterility control (Delsink et al., 2002; Middleton et al., 2003). However, these methods may be difficult for conservation organisations to adopt for managing populations of threatened species. They may be logistically infeasible, in conflict with the goals of the organisation, or distasteful to the general public. Moreover, the threatened status of the reintroduced species means that any management actions must carefully consider public reaction and must be based on empirical data. Removing one third of the population at two different periods after release appeared to briefly stabilise the bettong population but failed to reduce population size over a sustained period. Using the estimated growth rate from this study, one third of the population would need to be removed every year in order to stabilise the population. This would be easier to achieve when the population is small, suggesting that early intervention may be necessary to avoid overpopulation issues in future reintroductions. The addition of a native predator may constitute a more natural and efficient method of achieving a natural population density, particularly if there are few alternative locations available that may want to host removed excess individuals. The addition of native predators may need careful management to ensure population

extinction of the target species does not occur.

We suggest that reintroducing herbivores without the addition of native predators may lead to a prolonged post-release growth phase with sustained high growth rates, inflated densities and subsequent damage to vegetation. This damage needs to be considered in light of the ecosystem services that burrowing bettongs provide, including the provision of burrows for other fauna (Read et al., 2008), foraging pits that can increase carbon and germination levels (James et al., 2010) and possible control of woody weeds (Noble et al., 2007). Nevertheless, bettong densities at Arid Recovery were up to 10 times higher than in wild populations in more productive habitats and continue to increase, suggesting that the population is currently unsustainable and that management intervention is needed if further impacts to in situ fauna and flora are to be avoided. Conservation managers should consider future overpopulation issues when introducing herbivores into fenced reserves and ensure that triggers are identified and management plans are in place for responding to overpopulation prior to translocations commencing. We strongly suggest that macropods are not reintroduced into conservation reserves without the presence of or planned future reintroduction of effective native predators and that, globally, practitioners ensure that an overpopulation management plan is prepared for any herbivore reintroductions into confined areas. Depending on the species, predators may need to be reintroduced after herbivores reach pre-determined levels and monitoring programs should be implemented to monitor predation impacts on species prone to overabundance as well as rarer in situ species. Ideally, reintroduction programs into restricted areas should endeavour to reintroduce species from all trophic levels, including predators, to maintain ecosystem balance.

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