

Predation by feral cats key to the failure of a long-term reintroduction of the western barred bandicoot (*Perameles bougainville*)

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Abstract

Context. Reintroduction of endangered species potentially places them back in contact with putative factors of historical decline, inadvertently providing the opportunity to evaluate their impact.

Aims. To monitor the long-term progress of a population of western barred bandicoot reintroduced to mainland Australia and to assess factors involved in its eventual local extinction.

Methods. Bandicoots were reintroduced from offshore Dorre Island to the nearby mainland peninsula of Heirisson Prong in 1995. The narrow neck of the peninsula was fenced to exclude foxes and feral cats from a 1200 ha area, but the area was subject to periodic incursions. There was parallel management of a confined but unsupported population in an *in situ* 17-ha predator refuge. Bandicoots were assessed for abundance, body condition and reproduction two to four times annually between 1995 and 2010. In addition, perceived threatening processes (drought, disease and the abundance of cats, foxes and rabbits) were monitored.

Key results. Bandicoots became well established at the site, spreading to all available habitat. Numbers fluctuated strongly, peaking at ~250 in 1999 and then declining to apparent local extinction (with subsequent re-establishment from the refuge), and at ~470 animals in 2006, followed again by extinction.

Conclusions. Predation by feral cats was implicated as the primary cause of both free-range extinctions and the eventual elimination of all bandicoots from the predator refuge. Other contributing factors in one or more of the declines were a reduction in reproduction and recruitment in bandicoots during a one-in-100-year drought, the impact of overabundant European rabbits on vegetation used by bandicoots for nesting shelter and brief fox incursions at key times.

Implications. Existing methods of control of feral cats are rendered ineffective in the presence of abundant and diverse native fauna and abundant exotic species (particularly European rabbits). In addition, episodic drought in arid Australia intensifies the impact of predation by restricting reproduction of prey species. These factors hamper the attempts of conservation managers to re-establish vulnerable species at sites other than those with the infrastructure and/or management intensity to largely exclude exotic predators (and preferably European rabbits) over the long-term.

Additional keywords: peramelid, extinction, predator-proof fence.

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Introduction

The role of the fox (*Vulpes vulpes*) in the decline of many Australian mammal species, as well as in the failure of many recent reintroductions, is now well established (Friend 1990a; Kinneer *et al.* 1988, Short *et al.* 1992; Short 1998). However, the role of the feral cat (*Felis catus*) in the early historical decline of many Australian mammal species remains contested (Low 1996; Flannery 2003; Abbott *et al.* 2014), with implications for the diagnosis of threatening processes and subsequent management focus in current reintroductions of such mammals. However, there is an increasing body of evidence attributing failure of reintroductions in arid and semi-arid Australia to cat

predation (Christensen and Burrows 1994; Gibson *et al.* 1994; Priddel and Wheeler 2004; Moseby *et al.* 2011). More recently, Woinarski *et al.* (2014) suggested predation by feral cats was the greatest threat to the survival of more than 100 extant native mammal taxa and likely responsible for the extinction of 28 taxa. They based this on assessments of known or presumed threats identified by expert opinion.

The western barred bandicoot (*Perameles bougainville*) is a small, delicate peramelid marsupial that formerly occupied much of the southern inland of Australia, but has only survived on two islands off the Western Australian coast. The last specimens recorded on mainland Australia were in the late 1920s and

early 1930s (Rawlinna in Western Australia in 1929 and in north-west South Australia in 1931: Copley *et al.* 1989; Friend 1990b). Its ecology on Dorre and Bernier Islands has been documented by Short *et al.* (1997a, 1998). *P. bougainville* is listed as 'endangered' by the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* and as 'vulnerable D2' in the recent action plan for Australian mammals (Woinarski *et al.* 2014).

The translocation of western barred bandicoots from Dorre Island to Heirisson Prong at Shark Bay on mainland Western Australia in 1995 was the first attempt to translocate this species, although a sister endangered species *P. gunnii* had been subjected to several largely unsuccessful translocations in south-eastern Australia dating to 1989 (Winnard and Coulson 2008). Subsequently, *P. bougainville* has been translocated to an inshore island in Shark Bay and to a site fenced to exclude predators and rabbits in arid South Australia (Richards 2007; Moseby *et al.* 2011).

Subfossil records suggest that the species was formerly widespread on the Shark Bay mainland (Baynes 1990), but there is little evidence for the timing of its demise in this region. The type specimen was collected on Peron Peninsula at Shark Bay in 1818 (Ride *et al.* 1962). Heirisson Prong is a community-managed reserve on a peninsula on the southern shores of Shark Bay, ~100 km to the south of Dorre Island. A predator-proof fence was constructed across the peninsula in 1989 with the aims of creating a reserve free of foxes and feral cats, and to allow reintroductions of threatened mammals (Short *et al.* 1994). The early years of the establishment of bandicoots on Heirisson Prong (to October 1999) were documented by Richards and Short (2003). The aim of the current study is to describe the dynamics of the reintroduced population from reintroduction in 1995 through to eventual local extinction in 2008, and to understand the environmental factors and management failings that contributed to this extinction. This study builds on earlier attempts to reintroduce endangered mammals to arid Australia, but differs from these in that it deals with the fate of a well established, widely distributed and abundant population subject to a variety of threatening processes, including that of predation from feral cats.

Methods

Study area

Heirisson Prong (26°3.503' S, 113°22.481' E) is a peninsula that juts into Shark Bay on the mid-west coast of Western Australia (Fig. 1). The conservation reserve is 1200 ha, located at the northern tip of the peninsula, and bounded on its southern margin by a 2.1 km long predator-proof fence that crosses from coast to coast and extends ~700 m across shallow tidal flats on the eastern coast. Here it runs parallel to a causeway that extends 2 km into the bay to a small island that is used as a stockpile by a salt harvesting operation. This salt operation, and the associated town of Useless Loop, 4 km south of the fence, provided a logistic base for the project. For much of the project duration, Heirisson Prong formed part of the 805 km² Carrarang Station (a pastoral property running goats for live animal export), but was returned to the State

Government in January 2008 (McCluskey 2008) to allow a tenure more in keeping with its role for conservation. It has been managed for conservation since 1989 by the Useless Loop Community Biosphere Project Group, a small group of dedicated volunteers from the mining community of Useless Loop.

The landforms of the peninsula include sand dune and sand plain habitat. Vegetation consists of coastal heath (dominated by *Thryptomene baeckeaceae* and *Melaleuca cardiophylla*) and shrubland (dominated by *Acacia tetragonophylla*, *Acacia ligulata*, *Pittosporum phylliraeoides*, *Alectryon oleifolius* and *Atriplex bunburyana*). Annual rainfall at Denham (22 km to the north-east) averaged 224 mm over the 109 years to 2009, with ~70% falling in May to August (www.bom.gov.au). Winter rainfall is typically reliable, but occasionally fails (approximately one year in ten will receive less than 50% of the average of 155 mm for the May to August period). Low winter rainfall occurred in 2001 (79 mm), 2006 (41 mm), 2007 (90 mm) and 2008 (55 mm) during the period of this reintroduction. Annual rainfall can be boosted by cyclonic rainfall, typically in late summer or early autumn. Examples for the period of study include the 208 mm and 250 mm that fell in March 2000 and March/April 2008 respectively. Such rainfall occurs in about one year in ten.

Heirisson Prong was managed to exclude and/or control foxes and feral cats. The barrier fence was built in 1989, and was partially rebuilt and repaired at various times since (Short *et al.* 1994; Short and Turner 2000). It became increasingly dilapidated through corrosion over its entire length and wave action at each end. It was mostly replaced in late 2001, but extreme low tides extending >1 km from the shore across a shallow tidal flat periodically exposed one end, allowing entry of foxes and feral cats. The fence was never an effective barrier for most of its life, requiring a higher level of maintenance and replacement in the marine environment than what the local community was able to deliver. Consequently, there were occasional incursions by foxes and some level of cat presence north of the barrier fence for much of the 13 years of this reintroduction, despite major efforts to eradicate them (Short and Turner 2005).

A 17-ha yard system surrounded by another predator-proof fence was located within the main reserve, which acted as an initial release location as well as a predator refuge at times of incursions by foxes or feral cats into the main reserve. This was more secure than the barrier fence, as it was constructed in a square and so had no exposed ends.

European rabbits (*Oryctolagus cuniculus*) and house mice (*Mus domesticus*) were present throughout the site, with numbers fluctuating greatly over time (e.g. Robley *et al.* 2002 for rabbits). Rabbits, in the absence of predation from foxes and feral cats, at times built to high numbers, overshooting their food supply. At these times they climbed into shrubs to feed, particularly *Acacia* species, defoliating and often eventually killing many (Richards 2004). There was also a population of burrowing bettong (*Bettongia lesueur*) reintroduced to the site in 1992 (Short and Turner 2000) and a suite of native rodents (*Pseudomys hermannsburgensis*, *Pseudomys albocinereus*, *Rattus tunneyi*, and reintroduced *Leporillus conditor*) that varied in abundance over time.

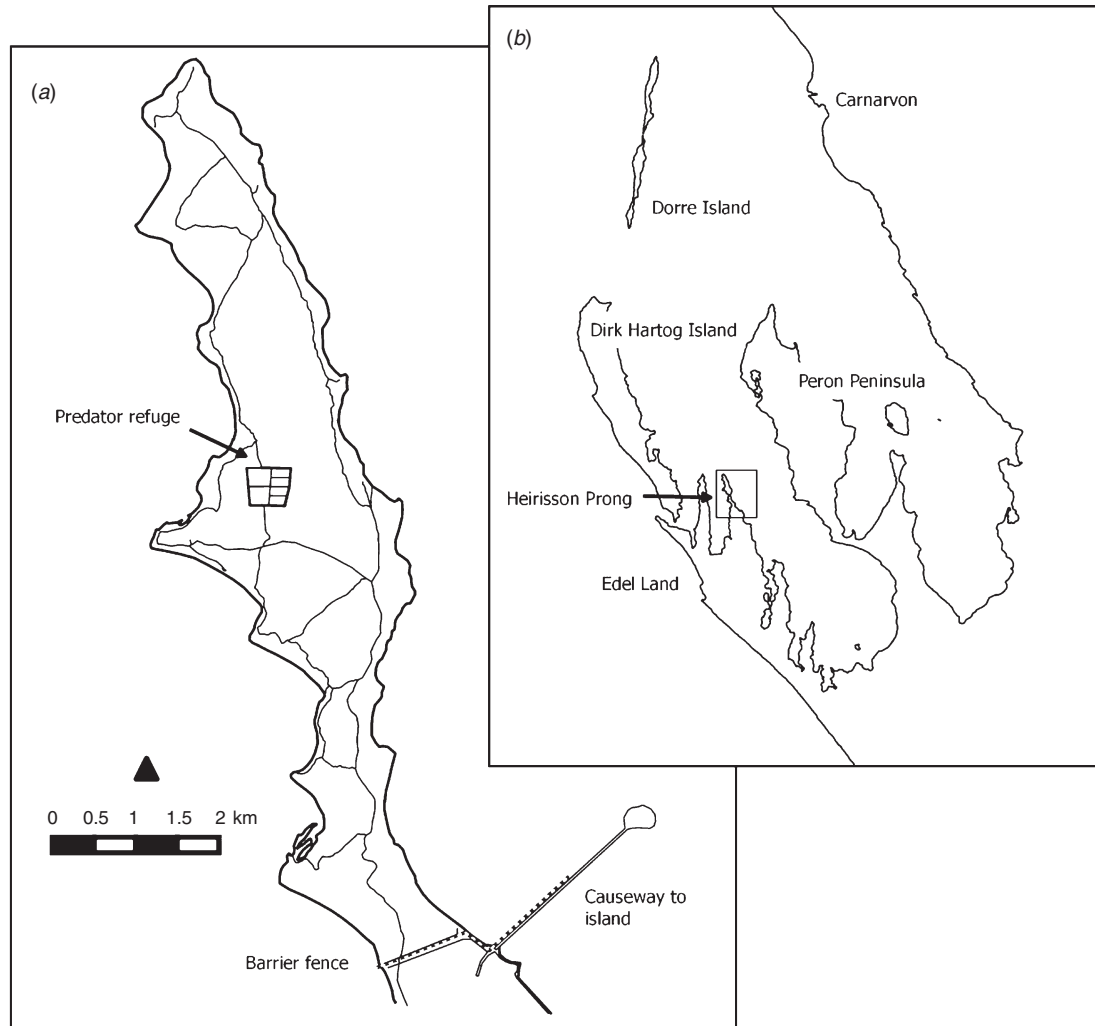


Fig. 1. (a) Map of Heirisson Prong showing the location of the barrier fence, the predator refuge, and vehicle tracks. (b) the location of Heirisson Prong at Shark Bay, Western Australia.

Translocation and animal husbandry

Details of the translocation of western barred bandicoot to Heirisson Prong in 1995 and 1996 are given in Richards and Short (2003). The population on Heirisson Prong was monitored quarterly by trapping until October 2002 and twice annually thereafter. Abundance of free-range bandicoots was assessed by intensive trapping along a ~40 km track network within the reserve. Cage traps were set at 100 m intervals and each location was trapped for two nights. Data comes from 47 trapping sessions between August 1995 and September 2010, totalling in excess of 25 000 trap-nights.

Bandicoots were marked individually using either ear punch (in years before 2001) or passive implant transponders (PIT tags) (Microchips Australia Pty Ltd, Melbourne) in subsequent years. Animals were weighed and measured. The ear punch or PIT number, location, gender, reproductive status and pes length were recorded for each individual. Data were used to calculate estimates of 'minimum-number-alive' (MNA) (Krebs 1998) and abundance, based on mark-recapture (Jolly-Seber full model: Krebs 2002). Reproductive output was assessed as

described by Richards and Short (2003). Body condition was assessed using the methodology of Krebs and Singleton (1993), and employed the formula of Richards and Short (2003). The exponential rate of increase of the population was calculated by utilising successive Jolly-Seber estimates of the population in the formula $\ln N_t - \ln N_{t_0} = rt$ (Caughley 1977), where N is the number of bandicoots at time t and r is rate of increase.

A small population of bandicoots was maintained within the 17-ha predator refuge for much of the life of the reintroduction. Bandicoots within the refuge were monitored by intensive trapping as described by Richards and Short (2003). Other than on establishment, no food or water was supplied to this subpopulation. Radio-collars were used at the time of first release of bandicoots (Richards and Short 2003), but associated mortality precluded ongoing use.

The bandicoot population was screened for disease by veterinarians from the regulatory authority and from Murdoch University at various times during the course of the reintroduction. This was in response to health issues identified in captive or extant populations elsewhere.

Reserve management

The presence of foxes and cats in the reserve was assessed by searching for prints on sandy tracks and by spotlighting. The search for prints was facilitated by the use of a drag towed behind a vehicle to clear existing prints from tracks. Spotlighting was conducted from the rear of a four-wheel-drive truck along a 20–30 km section of track each night, usually for three nights. Spotlighting typically occurred three or four times annually but was only conducted sporadically after May 2005.

Poison baits (120 g of dried meat containing 4.5 mg of sodium monofluoroacetate poison, or '1080') were typically laid monthly in the reserve and twice yearly in a 200 km² buffer zone to the south of the fence from 1993 (Short *et al.* 1994; Short and Turner 2000). This baiting program was designed to minimise the number of foxes in the buffer zone, reduce the likelihood of their breaching the fence and to ensure that any foxes that did breach the barrier fence were short-lived. However, this baiting intensity was gradually reduced in both area and frequency due to dwindling resources for management and difficulties in accessing baits. Regular monthly baiting of the reserve using meat baits ceased in November 1996 and was replaced by the use of meat baits only in direct response to fox sign within the reserve. In April 2006, the baits used in the buffer zone were changed from meat baits directed at foxes to experimental sausage baits directed primarily at feral cats (Algar *et al.* 2007). Additionally, the area baited was reduced to 100 km² and the frequency to once annually. Aerial baiting was conducted by the Department of Environment and Conservation, but was missed in some years due to various logistic difficulties or funding shortfalls.

Feral cats were far more difficult to control. The variety of methods used included laying out mouse carcasses with an oat grain coated with 4.5 mg of 1080 embedded in their throats (Short *et al.* 1997b). These were placed out at typically 100–200 m intervals around the track network. Other methods of control included Victor-soft catch traps and cage traps (Short *et al.* 2002b), cage traps on stilts (to exclude bettongs) and shooting. All trapping methods were ineffective at times when bettongs were present, and particularly so when they were numerous. Shooting was hampered by abundant shelter available to cats and by their inherent wariness. Ongoing fox control south of the barrier fence resulted in an increase in cat

density and greater pressure on the barrier fence (Short and Turner 2005).

Rabbit control using '1080' one-shot oats was conducted annually to 1995 but was discontinued thereafter due to the perceived risk to bandicoots. *Perameles bougainville* has an approximate LD₅₀ of 9 mg 1080 kg⁻¹ (Twigg and King 1991) and a small bodyweight, so would likely receive a lethal dose from eating one poisoned grain of oat. Rabbits were removed from the predator refuge by cage trapping in the years 1995–98 and 2002 in response to perceived high numbers and over-browsing.

Data analysis and assessment of causation

Data are presented for the life of the reintroduction, and then compared and contrasted for 1-year periods on either side of the two prominent peaks in bandicoot numbers. This serves to establish which life history parameters and which environmental factors varied between the growth- (rate of increase positive) and decline-phases (rate of increase negative) of the population.

An attempt was made to establish primary and secondary causes of bandicoot declines at the site using both induction and deduction (Pirsig 1999). Induction involved assessing which potential causal factors were operating in all three examples of documented decline to local extinction, on the assumption that the primary cause in each case would be the same. Deduction involved comparing measured results with *a priori* expectations of how density, reproduction and condition of bandicoots would change in a population subject to differing agents of local extinction. These expectations, based on general principles, are given in Table 1.

Results

Bandicoot numbers

Twelve animals were translocated from White Beach on Dorre Island in November 1995 and a further two in August 1996. Bandicoots were initially housed in the 17 ha predator refuge (Fig. 1). Ten bandicoots were released from there to free-range in May 1997. Another 72 were transferred from the predator refuge over subsequent years (Table 2). Plots of their abundance over time as free-range animals and in the predator refuge are given in Fig. 2a. Some bandicoots were returned to the predator

Table 1. *A priori* expectations of how various threatening processes would impact on attributes of bandicoot ecology

Potential threatening processes	Numbers	Reproduction	Condition
Predation (feral cats)	Declines coincide with a period of cat presence, particularly of high numbers and/or breeding	Maintained or increasing in response to greater resources per head	Maintained or increasing in response to greater resources per head
Predation (foxes)	Declines coincide with a period of fox presence	As above	As above
Drought	Declining	Declining	Declining
Rabbits via destruction of shelter	Declines commence/concentrated/greatest level in summer at times of temperature extremes	Not likely to affect early stages of reproduction where young in pouch cf later stages if young needs to be left in nest; failure in recruitment	Not likely to affect foraging, so no impact on condition
Rabbits via supporting predator numbers	Declines concentrated at times of transition from rabbit kittens present to absent	Maintained or increasing	Maintained or increasing

refuge at times in response to high cat numbers (Table 2). There were periods when bandicoots were present at such low numbers in the free-range population that they were not detectable by trapping (May 2001–April 2003, May 2007–May 2008, and post October 2008). The last record of a free-range bandicoot was in October 2008, 11 years after first release to free-range.

The trajectory of abundance of the free-range population showed marked peaks and troughs. The Jolly–Seber mark–recapture model suggested peaks of 252 bandicoots in December 1999 and 467 in May 2006 (Fig. 2a). MNA estimates closely mirrored the Jolly–Seber estimates but failed to capture the peaks. The decline in bandicoot numbers following each peak was precipitous. Only a single free-range animal (a male escapee from the predator refuge) was caught between May 2001 and April 2003 (seven trapping sessions totalling 4500 trap-nights). Bandicoots appeared to only persist in the predator refuge. A similar rapid collapse in numbers was evident also after the second peak. As many as 168 free-range individuals were caught in May 2006 at the rate of 44 per 100 trap-nights (56% trap success with capture of other species). However, this fell to just five individuals in January 2007 (1.6 per 100 trap-nights; 18% with other captures), and no animals in May 2007 (515 trap-nights), November 2007 (462 trap-nights) and May 2008 (441 trap-nights). A single adult female was caught in October 2008 in 503 trap-nights. She was unmarked, weighed 360 g and had no young – very atypical for the species at this time of the annual cycle, suggesting an absence of males. No bandicoots were caught in subsequent monitoring in May and September 2009 and February 2010 (a total of 1498 trap-nights).

Some bandicoots were maintained in the 17-ha refuge for much of the life of the reintroduction (Fig. 2a). The refuge had a population of 12 in November 1995 and reached a peak of 24 in June 1999, before being reduced to near zero in November 1999 following releases to supplement the free-range population. Some fifty bandicoots had been released to free-range up to this

Table 2. Western barred bandicoots released to free-range on Heirisson Prong from the predator refuge

Negative values indicate bandicoots being returned to the predator refuge from free-range

Date	Male	Female	Total
May 1997	5 (-2)	5 (-1)	11(-3)
June 1999	2	0	2
August 1999	5	20	25
September 1999	3	9	12
October 1999	2	0	2
November 1999	1	0	1
July 2000	4	3	7
October 2000	(-1)	(-1)	(-2)
January 2002	2 (-2*)	0	2 (-2)
July 2003	4	3	7
November 2003	1	1	2
May 2004	3	0	3
October 2004	4	6	10
January 2007	(-2)	(-1)	(-3)
Total	36 (-7)	46 (-3)	82 (-10)

*escapees from predator refuge.

time. Numbers in the refuge grew through 2001 and 2002 from a residual population of juveniles to a high of 21 in June 2002. Numbers of bandicoots were again reduced in the refuge by transfer of 22 bandicoots to free-range through 2003 and 2004 to re-build the free-range population. A small population remained in the refuge, building to 18 animals in January 2006. The refuge was breached subsequently by a feral cat; all known bandicoots within the refuge (a minimum of 14 at August 2006) were eliminated by the time she and her litter of eight dependant kittens were removed in October.

The Jolly–Seber estimates suggest free-range bandicoots on Heirisson Prong peaked at ~0.4 per hectare. The unsupported population in the predator refuge attained a size of 18–24 animals on four occasions (February and June 1999; June 2002, and January 2006); a density of >1 per hectare. This discrepancy in densities may partly be explained by the standard trapping lines on Heirisson Prong not sampling all available habitat of bandicoots, primarily due to the small home ranges of females (Richards and Short 2003), and partly by ongoing predation on the free-range population.

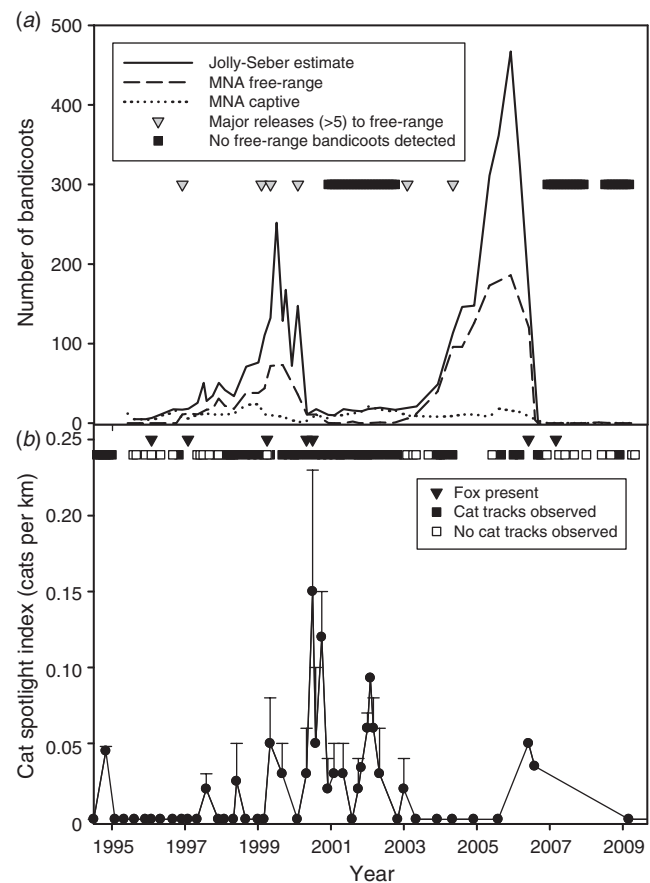


Fig. 2. (a) Number of captive and free-range western barred bandicoots on Heirisson Prong between November 1995 and September 2009. Jolly–Seber mark–recapture estimates are for the total population. Minimum number alive (MNA) estimates are given for the free-range population and captive population separately. (b) the presence of feral cats and foxes on Heirisson Prong during the period of the bandicoot reintroduction as indicated by spotlighting and track surveys.

Population growth

There were two periods of strong growth in the bandicoot population: one in 1998–99 and another in 2004–06 (Fig. 2a). In the first, the population grew from an estimated 34 to 252 in 14 months ($r=1.72$; population-doubling time of ~5 months) and in the second the population grew from an estimated 49 to 467 in 25 months ($r=1.08$; doubling time of ~8 months).

Similarly, there were two periods of rapid negative growth. The population decreased from an estimated 252 individuals in December 1999 to 11 individuals in October 2000. This gave a rate of decrease of -3.75 and a halving time for the population of 2.2 months. The second period of negative growth was from the peak of 467 individuals in May 2006 to 160 individuals in November 2006 and 4 individuals in January 2007. This gave rates of decrease of -2.14 over 6 months and -7.14 over 8 months. Halving times for the population were 3.9 months

when estimated over 6 months; 1.2 months when estimated over 8 months and indicates a greatly accelerating rate of decline over summer.

Bandicoot condition

The condition of bandicoots was not significantly different across increase and decrease phases centred on December 1999 (mean ratio of observed to predicted weight of 1.04 cf. 1.01: $F_{1, 436}=2.79$, $P=0.096$). However, condition of bandicoots was significantly higher in the increase phase pre-May 2006 (mean of 1.05 cf. 0.98: $F_{1, 615}=14.05$, $P<0.005$) relative to the corresponding decrease phase (Table 3).

Bandicoot reproduction

There were 815 measurements of the reproductive status of females over the life of the reintroduction, with 62% having

Table 3. Summary of parameters of bandicoot population and environmental factors immediately before and after peaks in bandicoot numbers in 1999 and 2006

Data covers 12 months on either side of peaks in December 1999 and May 2006. Major differences shown in bold

Attribute	Increase phase to December 1999	Decrease phase from December 1999	Increase phase to May 2006	Decrease phase from May 2006
Numbers of bandicoots	Growing strongly with doubling time ~5 months	Declining rapidly, halving time ~2.2 months	Growing strongly with doubling time ~8 months	Declining rapidly, halving initially every 3.9 months, accelerating to every 1.2 months.
Condition of bandicoots	Above average with overall mean of 1.04. ($n=236$)	Above average with overall mean of 1.01 ($n=201$)	Above average with overall mean of 1.05 ($n=443$)	Below average with overall mean of 0.98 ($n=173$)
Reproduction of bandicoots	67.3% females with pouch young /large nipple ($n=147$); pouch young/ large nipple per female = 2.02 ($n=99$); smallest female with pouch young 207 g	58.4% females with pouch young/large nipple ($n=89$), pouch young/ large nipple per female = 1.77 ($n=52$); smallest female with pouch young 207 g	75.0% females with pouch young/large nipple ($n=172$); pouch young/ large nipple per female = 1.84 ($n=129$); smallest female with pouch young 201 g	14.5% females with pouch young/large nipple ($n=68$); pouch young per female = 1.90 ($n=10$); smallest female with pouch young 230 g
Recruitment of bandicoots	134	62; 46% of the prior increase phase	181	73; 40% of the prior increase phase
Rainfall	259 mm, above the long-term median of 208 mm. Boosted by 136 mm in May 1999 (cf May median of 27 mm)	384 mm including 208 mm in March and 62 mm in May 2000; well above both median and average rainfall	288 mm; substantially above the long-term median. Heaviest falls in May and June 2005.	35 mm, driest 12 month period in the rainfall record and 16 successive months below mean rainfall
Rabbits	Low (<1 per km of spotlighting), increasing to <2 per km in spring	Low (<1 per km of spotlighting), increasing to <2 per km in spring	Moderately high (1.8–3.7 per km of spotlighting); rabbits climbing into shrubs with major defoliation in May 2006	Rabbits active and conspicuous during day with major defoliation of shrubs (Nov 2006); major decline to 0.5 km⁻¹ (Jan 2007) with the few rabbits visible during day sluggish and reluctant to leave solid shade; major die-off (Feb 2007), no sightings of live animals (May 2007)
Foxes	Incursion in Sep 1999	Incursions in Oct and Dec 2000, well after decline in bandicoots first detected	No incursions	Incursion in Nov 2006, well after decline of bandicoots first detected
Feral cats	Combination of results from track surveys and spotlighting suggest a very low density population. No cats removed	Spotlighting revealed major increase in cat population from Oct 1999; 1 cat removed Oct 2000 and 4 in early 2001	1 cat removed Apr 2005; no cats seen while spotlighting in May 2005 and Jan 2006	8 cats removed (with 6 in Feb 2007); cats seen during spotlighting in Nov 2006 and Jan 2007; some sparse cat sign still in early Mar 2007

pouch young or enlarged (generally lactating) nipples. The smallest female recorded with pouch young was 169 g, but only 10.4% of females 160–199 g ($n=77$) had pouch young or enlarged nipples. The proportion of females with pouch young or enlarged nipples increased with bodyweight (53.9% for females 200–239 g ($n=105$) and 80.2% for females 240 g and above ($n=479$)). The majority of records (66%) of adult females >240 g without young were in the hotter and typically drier months of November to February. The mean litter size (number of pouch young or enlarged nipples) per female with young was 1.86 (range 1–5; $n=505$).

The percentage of females with pouch young was marginally lower in the decline phase post-December 1999 (58.4 v. 67.3%) and dramatically so in the post-May 2006 decline (14.5% v. 75%) (Table 3). The average number of pouch young per female was not consistently lower in the decline phase relative to the corresponding increase phase. The size of females with young was similar across the increase and decline phase centred on December 1999. However, in the post-May 2006 period the smallest female with pouch young (230 g) was substantially larger than at other times.

Bandicoot recruitment

In total, 691 new bandicoots were captured and marked over 11 years to 2006 across both free-range and captive populations (Fig. 3a). The known number recruited to the population varied greatly between years, from lows of seven and nine in 1996 and 2003 respectively to a high of 176 in 2006. No recruitment was recorded in 2007 following the collapse of the population over the summer of 2006–07 and only one in 2008. The sex ratio of new recruits was male dominant at 1.29 : 1.

The subpopulation within the 17-ha predator refuge generated 110 of the new bandicoots marked on Heirisson Prong (~16%). The bulk of these (97) were before 2003. A high majority (82) of the 110 were transferred to free-range over the life of the refuge (Table 2).

Recruitment declined substantially in both decline phases of the population, relative to the previous 12 month growth phases (Table 3). The decline was 46% of the prior increase phase for the post-December 1999 period and 40% post-May 2006 period.

Health screening of bandicoots

The bandicoot population on Heirisson Prong was screened for disease by veterinary staff in June 2000 (toxoplasmosis, $n=7$), October 2002 (papilloma virus and chlamydia, $n=20$), and October 2005 and May 2006 (papilloma virus and chlamydia, $n=35$ and 29 respectively). No health issues were identified.

Potential factors impacting on bandicoot dynamics – drought

The annual rainfalls for the years 1995–2009 varied between a low of 85 mm in 2006 to a high of 383 mm in 2000. The long-term average for the site is 224 mm per annum. The variation of annual totals from the long-term mean are shown in Fig. 3b. Annual rainfalls in 5% of years in the rainfall record were <112 mm.

Runs of low rainfall years during the current study occurred from 2001 to 2003 (annual totals of 177, 162 and 129 mm

respectively) and 2006 to 2007 (annual totals of 85 and 114 mm). Below average rainfall extended for 23 months for the period July 2005 to May 2007. The failure of winter rain in 2006 and the absence of following rain contributed to the driest 12 month period (June to May) in the rainfall record (35 mm for the 12 month period).

Major increases in bandicoot numbers coincided broadly with consecutive years of average rainfall (1998 and 1999 for the first and 2004 and 2005 for the second). The first period of decline of the bandicoot population coincided with above-average rainfall in 2000; the second period with extreme drought (Table 3).

Potential factors impacting on bandicoot dynamics – rabbits

Rabbit numbers in October 1999, at the time of the first bandicoot peak, were moderate to low (1.67 km^{-2}). Spotlight counts of rabbit numbers in January 2006, just before the second peak in bandicoot numbers, were 3.7 km^{-2} , nearly twice that of the area south of the fence subject to fox and cat predation (1.9 km^{-2}). While comparatively high, these numbers were not exceptional.

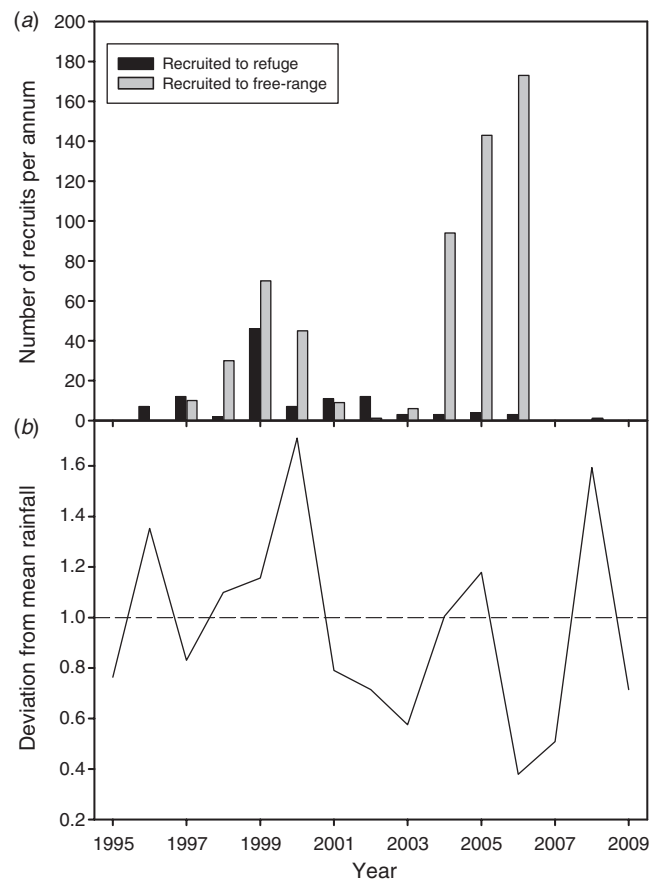


Fig. 3. (a) Annual recruitment of bandicoots on Heirisson Prong. Data are the sum of all new unmarked animals caught in a particular year, either in the predator refuge or as free-range animals. (b) Deviation of annual rainfall from the long-term average of 224 mm (data from Denham, WA). The dotted horizontal line equates to the long-term mean rainfall. The year 2006 was the second driest in the 109-year rainfall record.

Greater peaks during the life of the bandicoot reintroduction had been experienced in December 1997 (17.8 km^{-1}), October 2002 (4.95 km^{-1}) and October 2004 (5.26 km^{-1}). However, the moderate numbers of rabbits in combination with extreme drought from mid-2005 to mid-2007 resulted in a major impact on the vegetation, including the defoliation of a key shelter plant of the bandicoots, *Acacia tetragonophylla*.

Rabbits were present in the predator refuge for the duration of the bandicoot reintroduction. In total, 165 (9.7 ha^{-1}) were removed over the summer before the addition of bandicoots and extensive defoliation of shrubs was recorded in January 2002, during which 74 (4.4 ha^{-1}) were removed. At this time there were an estimated 13 bandicoots in the refuge with no adverse impact detected.

Potential factors impacting on bandicoot dynamics – fox incursions

There were six identified fox incursions into Heirisson Prong between January 1996 and September 2009, to give a rate of approximately one every 2.3 years. Incursions were apparent from fox prints along sandy tracks. Fox carcasses were rarely detected after baiting, with death inferred from the absence of fresh tracks. The estimated maximum durations of incursions (~20–130 days: Table 4) are likely to be substantial over-estimates of fox presence, as they depend largely on intervals between successive field trips when fox tracks were observed. For example, if fox tracks were evident on arrival, then the fox may have entered the reserve on any day back to the first after the previous field trip.

Two of the six incursions (July 1996 and August 2007) occurred at times when there were no free-range bandicoots. Of the others, one coincided with moderate growth in the bandicoot population (September 1999), one with a static population (July 1997) and two (October/December 2000, November 2006) with significant declines in the bandicoot population (Table 4).

Potential factors impacting on bandicoot dynamics – feral cats

There were 62 field trips to Heirisson Prong between the release of bandicoots to free-range in May 1997 and their near-total demise in February 2007. Some sign of the presence of feral cats (tracks, sighting during spotlighting, or a capture via trapping or shooting) was detected on 50 (81%) of these trips (Fig. 2b).

Table 4. Fox incursions at times when bandicoots were free-range, showing the estimated number of foxes and the maximum duration of their presence and the corresponding rate of increase for the bandicoot population calculated from MNA estimates

Date	Estimated number of foxes	Maximum duration of incursion	Bandicoot rate of increase (r)	Months over which r measured
Jul-1997	2 ^A	<130 days	0.00	5 months
Sep-1999	1	<23 days	2.96	2 months
Oct/Dec-2000	1	<120 days	-2.37	6 months
Nov-2006	1	<70 days	-20.41	2 months

^AOne carcass recovered after maximum of 60 days.

Spotlighting provided a quantitative index, but was prone to false negatives; there were 14 of 41 occasions when spotlighting gave a zero index when cats were known to be present from track counts or a capture. Cats were known to breed on Heirisson Prong in some years (2000, 2002, 2003, 2004 and 2006). Thus, bandicoots co-existed with feral cats for much of the period of this reintroduction. Intensive and persistent control actions (~15 000 trap-nights and 5000 cat baits over 12 years) kept cats at low densities, particularly during low rainfall years when trapping and baiting were more effective. Trap success for feral cats was inversely and significantly related to annual rainfall – presumably a surrogate for abundance of preferred prey (J. Short, unpubl. data). There were two major periods when cats escaped control efforts and their populations grew substantially – October 1999 to October 2003, and July 2006 to February 2007. The two major declines of bandicoots coincided with these.

Tracks of cats were regularly observed from August 1998, but only a single sighting of a cat was made in 17 nights of spotlighting spread over six sessions between August 1998 and August 1999 (mean of 0.004 km^{-1}), suggesting a very low density population contained by regular baiting. However, the cat population appeared to grow strongly thereafter, with five cat sightings in six nights of spotlighting in October 1999 and February 2000 (mean of 0.04 km^{-1} ; a 10-fold increase). Six cats were trapped or shot in the 12 months to October 2001 and it is likely that others were poisoned. The largest peak in cat activity, as assessed by spotlighting (March 2001: 0.12 km^{-1}), coincided with the final stages of the first decline in bandicoot numbers and the beginning of the 2-year period when no free-range bandicoots were detected. At this time, bandicoots appeared to persist only in the predator refuge where they were protected from predation.

In the second smaller peak in cat activity (2006–07), cat tracks were first detected in January 2006 and seen on all subsequent trips to February 2007. The spotlight index peaked at 0.05 km^{-1} in November 2006. Eight adult cats were trapped and removed between July 2006 and February 2007. Again, it is likely that additional cats were poisoned. Unfortunately, this peak in cat activity was accompanied by a breach of the predator refuge by a lactating female cat with the loss of all resident bandicoots by October 2006 (at least 14 bandicoots (0.82 ha^{-1}) in <14 weeks).

Discussion

Success followed by failure

Western barred bandicoots successfully established on Heirisson Prong following their reintroduction in 1995, building in number and dispersing to occupy all available habitat (Richards and Short 2003). They made use of dense, low, divaricating, often prickly shrubs for shelter, creating nests in shallow scrapes within the leaf litter under shrubs. Attributes of reproduction and condition at Heirisson Prong appeared similar to those on their island refuges (Short *et al.* 1998; Richards and Short 2003), affirming the quality of habitat despite >90 years of occupation by European rabbits. Bandicoots fed on a wide variety of insects, predominantly beetles, grasshoppers and crickets, as well as seeds, berries and skinks (Visser 2000).

The reintroduction to 1999 largely met the criteria for success as defined by Richards and Short (2003). However, numbers of bandicoots since that time have fluctuated greatly, rather than rising monotonically to an asymptote set by carrying capacity. Over the life of the reintroduction, the population of bandicoots oscillated between extreme growth (driven by high fecundity) and extreme decline (with high mortality). Clearly, environmental or biotic factors varied widely over time at the site. Possible factors were: year-to-year variation in weather (in particular, years of drought); wide variations in density of rabbits over time; fox incursions, typically of relative short duration; and cat incursions, leading in some cases to their establishment and breeding within the reserve. Unfortunately, the reintroduction of western barred bandicoots to Heirisson Prong ultimately failed in response to one or a combination of the above factors, with the last animal detected in October 2008, 13 years after their transfer to the site.

Two periods of decline compared

The two periods of collapse in bandicoot numbers differed in that reproduction and condition of bandicoots remained high in the first, but declined substantially in the second (Table 3). Hence, in the first, commencing approximately December 1999 and largely complete by February 2001, the decline appeared largely due to the high levels of predation exceeding recruitment. Track surveys and spotlighting indicated that feral cats were present and widespread during this period. Six cats (of which five were adults) were eventually removed between October 2000 and October 2001 (0.5 km^{-2} ; Fig. 2 in Short and Turner 2005). There was a fox incursion of brief duration (September 1999) that preceded the decline by several months and a more protracted one (October/December 2000) that overlapped the decline. The latter incursion occurred well into the decline (>8–10 months past peak numbers) and so was unlikely to have been the primary cause, although it possibly had some influence. Rainfall was average or above average in 1999 and 2000 and rabbits were at low levels (0.63 to 1.67 km^{-1} ; <40% of the rabbit index south of the barrier fence). Reduced recruitment of bandicoots in the decline phase suggested predation extended to juveniles as well as adults.

The collapse of the bandicoot population from peak numbers in May 2006 to near-extinction in February 2007 was associated with high numbers of feral cats and another fox incursion. In this case it was exacerbated by extreme drought, and severe defoliation by rabbits of shrubs used by bandicoots for shelter and nesting. Eight cats were trapped between July 2006 and February 2007 (2 adults and 6 subadults). Poison baits directed at feral cats were laid regularly during this period, presumably killing some cats (at minimum two adult females, mothers of two size classes of subadults caught during this period). This suggests a minimum density of cats of 0.83 km^{-2} . A fox incursion in November 2006 occurred some 5 months after peak bandicoot numbers and so is unlikely to have initiated the decline, but may have contributed to the subsequent loss of bandicoots. European rabbits were at moderate numbers in spring 2006 and early summer, but, due to drought, overshot their food supply. This resulted in them climbing into the canopies of shrubs, stripping them of leaves and ring-barking branches.

This defoliation, particularly of *Acacia tetragonophylla*, allowed the high winds, typical of summer at Shark Bay, to scour accumulated leaf litter from under shrubs, likely impacting the nesting and shelter sites of bandicoots. Rabbits were abundant and highly visible during the day in midsummer, sitting listlessly in solid shade and reluctant to flush (more than 60 were shot). However, by late February, few could be sighted and the bulk of the population was assumed to be dead from starvation and water stress.

Data comparing the 12-month periods before and after the May 2006 peak in the population (Table 3) show the following: (1) a rapid decline in the population of bandicoots, with rate of population decline accelerating over time; (2) a decline in body condition of bandicoots after the peak (from 5% above expected to 2% below – significant, but unlikely to be of sufficient magnitude to compromise adult survival); (3) a decline of the proportion of females with pouch young from 75% of the total before the peak to 15% after the peak; and (4) a decline in recruitment to 40% of the previous 12-month period.

Threatening processes – drought

Extreme drought is a recurring feature of arid and semi-arid Australia and is known to impact on the population dynamics of native species including the western barred bandicoot. Short *et al.* (1997a) documented a 75% decrease in bandicoot numbers on Bernier and Dorre Islands in response to a drought that extended from November 1986 to March 1989. Over 4 years, rainfall averaged 158 mm, which was 71% of the long-term average, and included two successive years with ≤ 125 mm. In another example, track counts of reintroduced western barred bandicoots declined by 50% during a drought period at an arid site in South Australia, despite the absence of rabbits and feral cats (Moseby *et al.* 2011).

Eastern barred bandicoots, too, are susceptible to drought (Seebeck 1979; Winnard and Coulson 2008), with the wild population at Hamilton in western Victoria declining markedly during the drought years of 1966–68. Low rainfall was believed to impact on *P. gunnii* in south-eastern Tasmania also, with a steady decline in numbers on trapping grids over 4 years when annual rainfall was ~80–93% of the long-term average over three consecutive years (Mallick *et al.* 2000).

Threatening processes – rabbits

European rabbits are the most conspicuous and abundant mammal species on Heirisson Prong, with sand dunes and sand plains providing ideal habitats. Rabbits occur throughout the landscape with spotlight indices over a 20-year period varying between 0.32 and 17.8 km^{-1} , a >50-fold variation (J. Short, unpublished data). Typical levels were likely boosted by the ongoing control of foxes and feral cats, the chief predators of the species (see Risbey *et al.* 1999 for a diet study). At peak densities over the summer of 1997–98, rabbits were estimated at 38 per hectare from warren entrance counts (Robley *et al.* 2002), and were defoliating and killing many shrubs. While most species recovered, little of the *Acacia ligulata* had regenerated ten years on.

There was no detectable decline in condition of bandicoots on Heirisson Prong associated with rabbit density, even with the

extreme densities of rabbits experienced in 1997 (Richards 2004). However, variations in litter size of bandicoots could be explained by a multiple regression that included rabbit density and rainfall over the previous 4 months (Richards 2004). A doubling of the rabbit index to 4 km^{-1} corresponded with a decline in litter size from 1.86 to 1.58.

Western barred bandicoots use concealed nests of leaf litter under shrubs to shelter during the day, which confer substantial thermoregulatory benefit and conceal the occupant from predators (Richards 2004). The defoliation of key shrub species is likely to have a major impact on their nest sites. *Acacia tetragonophylla* is one species that provides shelter for bandicoots at Heirisson Prong. Its combination of dense, prickly branches, leafy canopy extending to ground level and accumulated litter provides protection from both predation and extremes of temperature. The loss of this protection as a result of defoliation of the canopy is likely to have exposed the bandicoots to greater predation and thermal stress. The impact on the population from these stressors may have extended the typical period of anoestrus over dry summers, limiting the ability of the bandicoot population to replace numbers lost to predation.

However, *P. bougainville* have been observed using rabbit burrows (Richards 2004) as has *P. gunnii* (Heinsohn 1966). They have also been observed to nest in the *Thryptomene baeckeacea*, *Alectryon oleifolius*, and *Melaleuca cardiophylla* on Heirisson Prong (Richards 2004), species less impacted by rabbits. Hence, bandicoots are likely to have been flexible enough to deal with loss of cover and litter of their favoured *Acacia* nesting shrubs due to defoliation by rabbits and subsequent scouring of leaf litter by summer winds.

Rabbits are believed to impact on habitat for other *Perameles* species also. The removal of between 40 000–50 000 European rabbits from Woodlands Historic Park, a reintroduction site for *P. gunnii*, in 1993 coincided with a growth in estimated bandicoot numbers from ~90 in 1992 to a peak in 1994/95 of over 600 (Winnard and Coulson 2008). This management action coincided with years of above-average rainfall; both factors are likely to have improved ground cover, resulting in decreased vulnerability to predation as well as increasing food availability.

Threatening processes – fox predation

Foxes have invaded Heirisson Prong at a rate of about once every 2 years over the life of the project, with conspicuous impact on the reintroduced population of burrowing bettong being recorded by Short *et al.* (2002a). They detailed major instances of surplus killing of bettongs, but recorded no such instances for bandicoots. Meat baits were laid in response to fox incursions. Incursions were typically short lived (<1 to <4 months) and, unlike feral cats, there was no evidence of a pair establishing or breeding at any time during the life of the project.

While foxes may have played a contributory role in the decline of free-range bandicoots, they appeared not to have a primary role. There was no apparent link between the initiation or scale of decline of bandicoots and the timing or duration of fox incursions. The more cryptic behaviour of bandicoots (relative to bettongs and rabbits) and the ready availability of shelter in dense low, prickly shrubs are likely to have resulted

in lesser impact, although a severe short-term impact could have been disguised by the bandicoots' relatively high rate of increase. The impact of foxes on bandicoots may have been limited by their infrequent and short-lived incursions (of typically a single fox to the peninsula) and by the availability of high numbers of rabbits, bettongs, and other small mammals as prey.

Foxes are a known predator of *Perameles gunnii* at both wild and reintroduction sites in Victoria (Dufty *et al.* 1994; Hill *et al.* 2010). Seebeck (1979) presented anecdotal accounts of apparent surplus killing of eastern barred bandicoots by foxes near Hamilton in the early 1900s and predation by foxes was considered a major factor in the failure of reintroductions in Victoria (Winnard and Coulson 2008). The open grassland habitat utilised by *P. gunnii* may make them particularly vulnerable to a cursorial predator.

Threatening processes – predation by feral cats

Feral cats appeared to be the primary factor in the declines of bandicoots at Heirisson Prong, in both the free-range population post-December 1999 and post-May 2006, and the population in the predator refuge in October 2006. Moderate and/or high densities of cats coincided with periods of rapid decline of free-range bandicoots or periods where there were few or no free-range bandicoots. Estimated cat densities (minimum estimates based largely on captures only) during the two periods of loss of free-range bandicoots were <30% of the peak density of feral cats recorded on Heirisson Prong in 2002–03 (2.8 km^{-2} ; Short and Turner 2005), emphasising the broad food base available to feral cats in the absence of bandicoots. A single female cat appeared responsible for the loss of all bandicoots in the predator refuge.

While drought and overgrazing of vegetation by rabbits were clearly major contributing factors to the final collapse and eventual local extinction of the bandicoot population over the summer of 2006–07, it is unclear to what extent they were critical. Three observations suggest that feral cats, having escaped control efforts, were able to eliminate the bandicoot population regardless:

- The first collapse in the bandicoot population (in 2000) was associated with the sustained presence of cats (tracks present on every trip from October 1999 to through 2001), but not with drought or high rabbit numbers.
- All bandicoots were eliminated within the predator refuge by a female cat who had breached the fence within ~3 months to early November 2006, before summer and the peak of drought conditions.
- Cat densities at the time of both collapses in bandicoot numbers were well below peak densities recorded in the absence of bandicoots, emphasising the ongoing capacity of cats to target any remaining bandicoots.

It is likely that at least some bandicoots survived the summer of 2006–07, as a single female was caught 21 months later. However, these were not able to re-establish, despite the total collapse of the rabbit population by March 2007 and a gradual recovery of the vegetation following the breaking of the drought in winter 2007. It appears that surviving bandicoots were at such

low numbers that the last few individuals were unable to find each other to mate. This can be considered an example of the 'Allee effect' (Begon and Mortimer 1986), a destabilising inversely density-dependent effect contributing to the eventual local extinction of the population.

Unfortunately, there was little direct evidence for predation by cats on bandicoots at Heirisson Prong, in contrast to well established predation on rabbits; rabbits made up 88.4% of the diet of cats by volume on Heirisson Prong (Risbey *et al.* 1999), small mammals (Risbey *et al.* 2000) and burrowing bettong (J. Short, unpublished observations). The studies by Risbey *et al.* were conducted in the early 1990s, before the release of bandicoots to Heirisson Prong. However, cats are known to prey on bandicoots elsewhere and *P. bougainville*, with a mean adult weight of ~230 g (Short *et al.* 1998), falls within the preferred prey size of cats.

Domestic cats were reported to kill *P. gunnii* in a wild population persisting in semi-rural Hamilton in western Victoria, but road kills were found to be the major cause of deaths (Seebeck 1979; Dufty 1994). Cats appeared to favour juvenile *P. gunnii* (Dufty 1994). This species is substantially larger than *P. bougainville* (~1000 g; Mallick *et al.* 2000), and adults may be beyond the optimal size for cat predation (Pearre *et al.* 1998). Cats are also known to prey on long-nosed bandicoots (*P. nasuta*), with bandicoots making up 28% by volume of 20 cat stomach contents and scats samples collected from a Sydney population (Dickman 1996; Scott *et al.* 1999).

The loss of forty golden bandicoots *Isoodon auratus* reintroduced to the Gibson Desert in 1992 was attributed to predation by feral cats (Christensen and Burrows 1994). Bandicoots occupied dense spinifex and gained an average of 40% of bodyweight within 2 months of release. Females carried pouch young, suggesting suitability of habitat. No direct evidence of predation by cats was found (largely due to the rapid shedding of radio-collars by bandicoots) but it was considered likely, due to the high density of cats present and evidence of cat predation on bettongs (*B. lesueur*) released at the same time.

Threatening processes – disease

Diseases have been identified in *P. bougainville* (Warren *et al.* 2005; Woolford *et al.* 2008) but are confined to the Bernier Island population and captive populations sourced from Bernier Island. Toxoplasmosis infections have been detected in a wild population of *P. gunnii* (Obendorf and Munday 1990). However, no disease or parasite issues were identified in the Heirisson Prong population.

Exotic disease has been suggested as the cause for the early historical demise of native mammals, including *P. bougainville*, in Western Australia (Abbott 2006). Abbott speculated that this disease had its origin in the pearling camps on Heirisson Prong in the 1870s, before radiating out from there to impact a wide range of marsupial and rodent species (as many as 33 species) across Western Australia. However, with the early pearling settlements would have come domestic cats and they would have rapidly moved beyond the settlements to exploit the rich rodent and marsupial fauna. Given what we know about the vulnerability of bandicoots to cat predation in this environment, the abundant native fauna at the time – collectively comparable

in density to the present day rabbit population (Short *et al.* 1997a), much of which was within the preferred prey size range for feral cats – and the regularity of drought (with the effect of suppressing breeding by bandicoots), it seems unnecessary to seek such an alternative explanation for the historical decline of bandicoots.

Predator refuge and in situ breeding facility

The predator refuge on Heirisson Prong was important in providing additional security and a ready source of animals to re-establish the free-range population after the initial decline. There were problems with intraspecific aggression in this species when confined (Richards and Short 2003), but despite this a small population of up to 24 animals was able to be maintained without food supplementation.

P. bougainville was translocated to a similar predator refuge (*in situ* breeding facility) at Dryandra Woodland in south-west Western Australia (Friend and Beecham 2004). A total of 27 animals sourced from Bernier and Dorre Islands, Heirisson Prong and a captive population were transferred to a 20-ha predator-proof enclosure within Dryandra with the intention of eventual release to free-range. Initial animals were transferred in 1998 and shared the enclosure with four other species. The colony was compromised by disease issues (wart-like syndrome), predation by diurnal and nocturnal birds of prey and pythons and husbandry issues; it was eventually abandoned.

Western barred bandicoots (2 males, 10 females) were translocated from Bernier Island to a 10-ha 'breeding yard' at Roxby Downs in arid northern South Australia in 2001 before release to a 1400-ha fenced area free of foxes, cats and rabbits (Moseby *et al.* 2011). The resulting population has been extant for at least 8 years as assessed by track counts.

Small breeding pens (0.01–0.02 ha) have been used for breeding *P. gunnii* before release with limited success (Winnard and Coulson 2008).

Where to from here?

This study has shown that, for this species in this environment, there were multiple pathways to local extinction: predation by an exotic predator alone, and predation in conjunction with resource depletion by drought and exotic herbivore species. It appeared there was no effective refuge from cat predation for bandicoots on Heirisson Prong. Whether this was equally true for fox predation remains uncertain. There may be opportunities to counter this predation at some sites by increasing the extent and continuity of habitat that provides refuge from predation. This can be achieved by reducing grazing intensities of exotic herbivores or by reducing fire frequency, with the aim of limiting the success of hunting by cats. A complementary approach would seek to intensify cat control in times of developing drought.

Control of feral cats at Heirisson Prong was greatly hampered by an ineffective barrier fence and abundant populations of European rabbits and burrowing bettongs. The use of a fenced peninsula to exclude exotic predators, while superficially attractive due to the short length of predator-proof fence relative to area protected, was beset with problems of rapid deterioration of the fence due to wave action, corrosion of the fence subject to tidal influences and corrosion of the land-based fence due to wind-borne salt. Further, a shallow tidal flat

>1 km wide on the eastern coast created major difficulties in maintaining an effective barrier in sea water. Sites protected by predator-proof fences, whether peninsulas or exclosures, clearly require a reasonable ongoing budget directed primarily at fence maintenance. For example, the Roxby Downs fence is reported to have an annual monitoring and maintenance cost of \$25 000 (Hayward *et al.* 2014). In addition, the capital cost of fence replacement (as often as every 10–15 years in a maritime environment) requires ongoing funding. Such a high and ongoing need for funding could not be met by a local community group on Heirisson Prong.

The coastal dune and sandplain habitat supported extremely high densities of rabbits that were difficult to manage cost-effectively. Rabbits, bettongs and other small mammals showed strong cycles of growth and fall that were asynchronous with each other, ensuring that there was always some prey type available to cats. This limited the effectiveness of food-based control methods for feral cats. Future reintroductions would benefit from choosing a site less favourable to rabbits or where rabbits can be more readily controlled or excluded.

The presence of bettongs was detrimental to almost all control measures directed at cats and foxes. Their presence made it impossible to use leg-hold traps because of the inevitable non-target captures. In addition, they quickly filled cage traps set for cats and they rapidly removed all food-based lures or baits. Attempts to elevate traps beyond the reach of bettongs resulted in poor capture success for cats. The development of new methods of control that do not rely on food as an attractant and that are specific to feral cats would greatly improve management prospects.

The release to large, secure predator-proof enclosures is seen by most practitioners as a step to eventual release beyond the fence (e.g. Moseby *et al.* 2011; Hayward *et al.* 2014). With a view to this, it has been suggested that a key research objective should be the determination of threshold levels of predation that can be tolerated by species (Sinclair *et al.* 1998; Moseby *et al.* 2011). While laudable, such a goal largely ignores the strong cycles of drought in arid and semi-arid Australia that impact on reproductive output of endangered species, making them vulnerable to being overwhelmed by exotic predators. It also presupposes effective management techniques for the control of feral cats in the presence of abundant native mammals. In the absence of such techniques, investment in a secure fence may be far more cost-effective than the ongoing struggle to maintain feral cats (and foxes) at a threshold density beyond the fence.

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