Predator swamping and supplementary feeding do not improve reintroduction success for a threatened Australian mammal, *Bettongia lesueur*

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Abstract.   Broad-scale Australian mammal declines following European settlement have resulted in many species becoming regionally or globally extinct. Attempts to reintroduce native mammals are often unsuccessful due to a suboptimal number of founders being used, high rates of predation and a lack of knowledge of the reintroduction biology for the species concerned. We trialled predator swamping and supplementary feeding in an attempt to offset predation and improve reintroduction success for the burrowing bettong (*Bettongia lesueur*) in arid South Australia. We compared population longevity of a large release group (1266 animals) with five releases of smaller groups (~50 animals at each). We compared release sites with (*n* = 5) and without (*n* = 1) supplementary food to determine whether site fidelity, body condition and reproduction were affected, and whether these traits aided population establishment. Predator swamping did not facilitate reintroduction success, with no bettongs detected more than 122 days after release. While supplementary food increased site fidelity and persistence at release sites, bettongs failed to establish successfully at any site. Neither predator swamping nor supplementary feeding enhanced reintroduction success at our sites but results suggested that supplementary feeding should be explored as an aid to reintroduction success for Australian mammals.

Additional keywords: burrowing bettong, predator swamping, supplementary feeding, translocation.

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Introduction

Since European settlement in Australia, 28 terrestrial mammal species have been declared extinct and a further 21 are currently threatened with extinction (Woinarski *et al*. 2014, 2015). The introduction of feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) to Australia, combined with habitat fragmentation, land clearing, overgrazing, altered fire regimes, persecution by landholders/ hunters and competition with rabbits (*Oryctolagus cuniculus*) and domestic stock are all factors believed to have contributed to these drastic declines (Burbidge and McKenzie 1989; Morton 1990; Dickman 1994). Such broad-scale losses have led to attempts to mitigate threatening processes and reintroduce species to their former range (e.g. Short *et al*. 1992; Kingsley *et al*. 2012). Success rates for reintroductions and translocations in Australia are highly variable (Short 2009; Armstrong *et al*. 2015), with the outcome often dependent on the presence or density of predators at release sites (Short *et al*. 1992; Fischer and Lindenmayer 2000; Moseby *et al*. 2011; Short and Hide 2015). It is therefore vital that we identify factors that may improve reintroduction success, particularly in relation to predation (Griffith *et al*. 1989;

Short *et al*. 1992; Fischer and Lindenmayer 2000). As introduced predators are unlikely to be eradicated from Australia in the foreseeable future, identifying suitable reintroduction methods that allow populations to establish in the presence of introduced predators should be a priority for conservation programs.

Predator swamping (or predator satiation) occurs when the quantity of a prey species in a given area exceeds the potential number that can be eaten by local predators (Sweeney and Vannote 1982). It is especially effective when predators are territorial as the number of predators occurring within an area is limited (Sinclair *et al*. 1990; Gerber *et al*. 2003). Predator swamping is most often naturally observed through reproductive synchrony, whereby a prey species undergoes synchronised breeding events, resulting in a high probability that some juveniles will survive the threat of predation (e.g. Sinclair *et al*. 2000; but see Post *et al*. 2003). Predator swamping may have the potential to improve reintroduction success as the probability of predation of a particular individual is low, given the large group size (Götmark and Andersson 2005). Large release sizes (*n* > 100) can increase the likelihood of a successful

reintroduction (MacArthur and Wilson 1967; Wolf *et al.* 1996; Fischer and Lindenmayer 2000); however, this is not always the case (Short 2009). Mortality is usually highest in the period immediately after a translocation (Calenge *et al.* 2005; Hamilton *et al.* 2010), therefore large release numbers may compensate for these initial losses (Armstrong and Seddon 2008). The success of predator swamping as a reintroduction tool is often difficult to test due to the challenge in amassing large numbers of threatened species for release.

Supplementary feeding is considered a soft-release technique, allowing translocated animals to acclimatise to a new site before becoming independent (Bright and Morris 1994). A review of supplementary feeding studies found that translocated populations that received supplementary food had smaller home ranges, advanced breeding, increased body weight and higher population densities than populations at control sites (Boutin 1990). High reproductive rates may offset predation and enable population persistence, particularly when food in the environment is limited. Negative impacts associated with supplementary feeding may include predators targeting prey at feeding stations (Dunn and Tessaglia 1994), the consumption of supplementary food by non-target species (Moreno-Opo *et al.* 2012; Rickett *et al.* 2013), increased disease transmission (Robb *et al.* 2008) or dependence on supplementary food (Powlesland and Lloyd 1994; Robb *et al.* 2008). Supplementary food may aid in retaining a translocated species in an area where other factors, such as introduced predators, may be controlled (Rickett *et al.* 2013), or social interactions such as breeding may be facilitated (Armstrong and Seddon 2008; Hamilton *et al.* 2010). Dispersing individuals provide no genetic contribution to a population (Le Gouar *et al.* 2012), providing another reason for retaining a translocated population within a release area. Supplementary food is often provided only during an initial acclimatisation period after release and studies on the long-term benefits of supplementary feeding on reintroduced populations are limited.

Burrowing bettongs (referred to interchangeably as bettongs or burrowing bettongs) form part of a growing list of Australian species that now exist only where introduced predators are effectively absent, restricting them to offshore islands and fenced mainland reserves (Short and Turner 1992; Friend and Burbidge 1995). At <2 kg, burrowing bettongs fall within the 'critical weight range' (Burbidge and McKenzie 1989) of species that have been heavily impacted by the arrival of foxes and feral cats in Australia (Wood Jones 1924; Finlayson 1958). The outcome of previous burrowing bettong reintroductions has been largely determined by the presence or absence of introduced predators at release sites (Short *et al.* 2002; Moseby *et al.* 2011). We had an opportunity to determine whether predator swamping and supplementary feeding could be used simultaneously to offset predation and improve reintroduction success for burrowing bettongs, with potential applications for other critical-weight-range mammals. We compared large ($n > 1000$) and small ($n \approx 50$) release groups to test whether predator swamping could facilitate population establishment in the presence of low predator numbers (subject to control). We provided supplementary food at selected release sites to test whether it improved site fidelity, body condition and reproduction. We hypothesised that a large release group that was also provided with supplementary food was more likely to successfully establish than small release groups or release groups without supplementary food.

Materials and methods

Study species

The burrowing bettong is a social member of the Potoroidae family that lives underground in warrens or burrows during the day and is active above ground at night (Burbidge 1983; Short and Turner 1993; Sander *et al.* 1997). Historically, burrowing bettongs ranged over the southern two-thirds of Australia, but predation by foxes and feral cats, persecution, hunting and competition with domestic stock and rabbits led to burrowing bettongs becoming extinct on mainland Australia by the 1960s (Wood Jones 1924; Finlayson 1958; Short and Turner 2000).

Introduced feral cats, foxes and rabbits and naturalised dingoes (*Canis lupus dingo*) were all present at our study site. There is considerable debate as to whether dingoes suppress mesopredator (feral cat and fox) numbers or activity, thereby indirectly supporting small mammal species (Fleming *et al.* 2012, 2013; Johnson and Ritchie 2013). Extinctions have historically been lower where dingoes were present (Johnson *et al.* 2007) and direct persecution of feral cats and foxes by dingoes has been recorded (Moseby *et al.* 2012). Introduced rabbits are documented to have moderate dietary overlap with bettongs, yet the rate of increase in predator-free bettong populations is independent of fluctuations in rabbit populations, suggesting minimal competition (Robley *et al.* 2001, 2002). Rabbits may contribute to the decline of critical-weight-range mammals by supporting high numbers of introduced predators (Johnson 2006).

Study area

Burrowing bettongs were sourced from Arid Recovery (30°29′S, 136°53′E), a private reserve located 20 km north of Roxby Downs in arid South Australia. Dingoes, feral cats, foxes and rabbits were absent from the exclosures where bettongs were sourced (Moseby and Read 2006; Moseby *et al.* 2011). The reserve supported a self-sustaining population of bettongs in large exclosures of between 8 km^2 and 30 km^2, with the estimated total population size exceeding 3000 individuals across four exclosures (Arid Recovery, unpubl. data). Supplementary food was not provided to animals inside the reserve as adequate native vegetation was available.

The Release Zone was a 55-km^2 area encompassing four release sites, all of which were located on Stuart Creek Station (30°9′8″S, 136°57′30″E), ~10 km north of the northern boundary of Arid Recovery (Fig. 1). The station supports low cattle densities, and stock were excluded from the Release Zone several months before the translocation. Grazing damage due to stock was not evident at release sites. Dingoes were present and were not targeted for control as the release sites were north of the dog fence, where dingoes are not subject to eradication (Downward and Bromell 1990).

The dominant landforms at the source and release sites were longitudinal red sand dunes separated by clay interdunal swales. Vegetation on dunes was dominated by sandhill wattle (*Acacia ligulata*), hopbush (*Dodonaea viscosa*) and
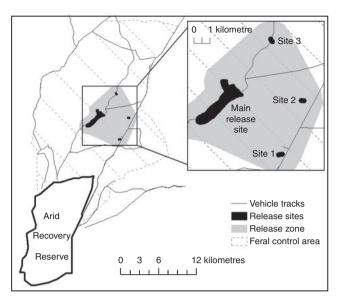
Fig. 1. Location of four release sites for bettongs within a single Release Zone on Stuart Creek Station, showing proximity to the source population (Arid Recovery Reserve). All locations were unfenced except the Arid Recovery Reserve, which was free of mammalian predators.

sandhill canegrass (*Zygochloa paradoxa*), while swales were predominantly chenopod shrubland (*Maireana astrotricha* and *Atriplex vesicaria*). Release sites were selected for having a large number of rabbit warrens (providing postrelease shelter for bettongs), extensive dune systems and good vegetation cover. Rabbit warrens at the release site included both active and inactive warrens at the time of the translocation. Previous bettong releases into areas with rabbits suggest that the two species can coexist (Robley *et al.* 2002; Moseby *et al.* 2011). No rabbit control was conducted before the bettong translocation. The climate was dry, with nearby Roxby Downs receiving an average annual rainfall of 151 mm between 1998 and 2013 (Bureau of Meteorology 2015). In the two months preceding the study (May–June 2013) the Roxby Downs region received 68 mm of rain, resulting in good vegetation condition, which provided food and shelter for bettongs at release sites.

Predator control

Intensive predator control targeting feral cats and foxes was carried out before, during and after the reintroduction. The 500-km^2 Feral Control Area included the Release Zone and surrounding areas (between 3 km and 10 km radius from release sites), although shooting was largely confined to the network of vehicle tracks within the area (Fig. 1). A total of 428 h was spent by Arid Recovery volunteers conducting spotlight shooting patrols throughout the Feral Control Area over an eight-month period from May to December 2013, including 62 h before the release of any bettongs. In all, 101 feral cats and 25 foxes were removed from the area during this eight-month period.

Reintroduction event

In total, 1492 bettongs were translocated from Arid Recovery to the Release Zone, comprising several smaller release sites, between July and December 2013. Bettongs were trapped inside

Arid Recovery in wire cage traps (Sheffield Wire Products, $220 \times 220 \times 550$ mm) partly covered with hessian sacks and baited with peanut butter and rolled oat balls or peanut butter sandwiches. Bettong trapping targeted specific sections of the reserve each night in an effort to maintain social and familial groups at all release sites. All bettongs were given uniquely numbered ear tags before release and morphometric data (weight, pes length, tail width, body condition and reproductive status) were recorded. Females with large pouch young were not translocated and were released at their point of capture inside the reserve. Bettongs were transported to the Release Zone in individual soft capture bags in vehicles. Travel to the Release Zone took ~1 h. Between two and 53 bettongs (mean = 23) captured in the same area at the source site were released at the same location (within a 1000-m^2 area) directly into premapped rabbit warrens (recorded on GPS devices) at least 2 h before sunrise on the same night of their capture. Up to four bettongs were released into a single warren, with a minimum distance of 10 m between release warrens.

Predator swamping

The predator swamping treatment group was released at the Main Release Site, a 250-ha unfenced area within the Release Zone (Fig. 1). In July 2013, 955 burrowing bettongs were released at the Main Release Site. Between 24 and 104 bettongs were translocated per night over 15 nights, with no more than 6 nights between releases. Subsequent translocations over three nights in August and again in October 2013 increased the total number of bettongs released at the Main Release Site to 1266 (Table 1). In October, smaller releases of between 48 and 56 bettongs occurred at each of three additional sites within the Release Zone (Sites 1–3) (Fig. 1; Table 1). The smaller release sites (Sites 1–3) were located ~4 km from the Main Release Site and from each other, but all sites were within the Release Zone and wider Feral Control Area (Fig. 1). Bettongs were released at one site per night. In December 2013, releases occurred again at Sites 1 and 3, with 39 and 29 bettongs released at each site respectively (Table 1). Bettongs had not been detected at either site for at least seven weeks prior to the second translocation to those sites.

Supplementary feeding

To assess whether supplementary feeding facilitated bettong establishment through increased bettong longevity and high site fidelity, these variables were compared both within sites and between sites. Within the Main Release Site (Fig. 1), five supplementary feeders with rolled oats were established at random locations on dunes before the translocation of bettongs. Feeders were positioned 250–1000 m apart and consisted of a vertical pipe (160 mm diameter $\times$ 1200 mm length) with an opening at the bottom that allowed rolled oats to spill into a plastic tray (400×600 mm). At each of these five feeders 10 track count plots (1×1 m) were randomly marked within 25 m of the feeder (treatment). Another 10 track count plots (1×1 m) were established at each of five control sites located ~200 m away from the nearest feeder but still within the Main Release Site. These latter plots were used to determine whether bettongs had also established in nearby areas where bettongs had been

Table 1. Releases of burrowing bettongs

Release information for bettongs translocated to the Release Zone on Stuart Creek Station in 2013. MRS, Main Release Site. Predator swamping treatments refer to either a large release group or a small release group

| Site | Release period | Treatment | | No. of males | No. of females | Total released |
		Predator swamping	Supplementary feeding			
MRS	Jul. 2013	Large	Food	539	416	955
MRS	Aug. 2013	Large	Food	73	58	131
MRS	Oct. 2013	Large	Food	98	83	181
Site 1	Oct. 2013	Small	Food	26	22	48
Site 2	Oct. 2013	Small	Food	34	22	56
Site 3	Oct. 2013	Small	No food	33	20	53
Site 1	Dec. 2013	Small	Food	17	22	39
Site 3	Dec. 2013	Small	Food	19	10	29
Total				839	653	1492

released but feeders were not close by. As bettongs were not released directly at feeders, bettongs observed using them were considered to have found them independently. Plots were cleared of existing tracks in the late afternoon using a broom. The following morning, all track count plots were checked for the presence of bettong, rabbit, dingo, cat and fox tracks. Each plot was monitored three times, with a four-day interval between each replicate.

An additional three supplementary feeders were set up 500 m outside the Main Release Site (and from each other) for a period of three weeks after the initial bettong release to monitor dispersal and to offer supplementary food to bettongs that were dispersing away from the Main Release Site. These three feeders were established in September 2013, two weeks after a supplemental release of bettongs at the Main Release Site (August) (Table 1), and the feeders remained in place during a supplementary release of bettongs in October. Two empty feeders 500 m from the Main Release Site were used as control treatments so that visitations by dispersing bettongs could be compared where food was and was not provided.

Nine feeders were deployed at the smaller release sites (Sites 1–3), with three feeders spaced 100 m apart at each site. These feeders consisted of an overturned plastic tub covering a food tray, with arched entrances cut out of each end to allow bettongs access to the food tray underneath. All feeders were positioned in the open but within 2–3 m of vegetation cover. Site 3 was a control site and therefore feeders there did not contain food.

Monitoring of population persistence

The persistence of bettong, rabbit and predator populations was monitored at all release sites using four methods: track counts, camera trapping, warren monitoring and trapping.

Track counts

Eleven track transects were established at release sites, with five inside the Main Release Site on dunes ($n = 3$, 1.54 km, 1.66 km and 1.22 km long) and vehicle tracks ($n = 2$, 0.38 km and 0.52 km long), two dune transects at each of Sites 1–3 (0.35 km each) and an additional two transects positioned on vehicle tracks 2 km outside the Main Release Site to monitor dispersal (0.29 km and 0.40 km long). All transects at the Main Release Site were a minimum of 100 m apart (monitored

monthly) and at Sites 1–3 were ~40 m apart (monitored every 1–2 weeks). To clearly observe tracks, a 1-m-wide steel bar was dragged across established transects on dunes and vehicle tracks within the Release Zone to clear existing animal tracks (Moseby *et al.* 2011). The following morning, the presence and number of bettong, dingo, cat, fox and rabbit tracks were recorded on each transect. If an animal's tracks left the transect and re-entered, it was counted both times to ensure consistency (Moseby *et al.* 2011). Transect counts were not conducted when the overnight wind speed exceeded 20 km h^{-1} as tracks quickly became obscured by sand. Transect monitoring commenced eight weeks before the bettong release and continued for six months after the initial release at the Main Release Site, and for 2–6 weeks after all evidence of bettong presence ceased at each of Sites 1–3.

Camera trapping

Remote cameras (Reconyx Hyperfire HC600 and HCO ScoutGuard SG560V) monitored 13 of the 14 supplementary feeders distributed amongst the four release sites. Additionally, up to 5 cameras were set opportunistically on vehicle tracks and warrens inside and outside the Main Release Site, but within the Release Zone, to monitor the presence and dispersal of bettongs. Supplementary feeders positioned 500 m outside the Main Release Site, both with food ($n = 3$) and without ($n = 2$), were also monitored by remote camera. In total, up to 23 locations utilised remote camera monitoring at some point during or after release. Cameras were set continuously after release and the presence of bettongs at feeders with and without food was compared by observing whether any bettongs used a particular feeder each day.

Warren monitoring

A thorough search within the entire Main Release Site enabled 106 rabbit warrens to be mapped before the bettong release. Following the release, subsets (mean = 54, range = 8–88) of these known warrens were monitored monthly by recording the presence or absence of tracks and scats of both bettongs and rabbits at burrow entrances. While not every warren was able to be monitored each month, any warren that had shown bettong activity in the previous month was included in the monitoring, in addition to other random warrens from the initial 106 identified. Any predator tracks or scats within 20 m of warrens

were also recorded. Ten warrens at each of Sites 1–3 were also mapped before releasing bettongs at those sites, and were monitored weekly.

Trapping

In November 2013, four months after the initial bettong release, two nights of cage trapping (160 trap-nights) was undertaken at the Main Release Site to monitor the condition, reproduction, number and distribution of bettongs. Traps were positioned around supplementary feeders known to have been frequented by bettongs. Trapping was conducted simultaneously over two nights at Site 2 (60 trap-nights), one month after the release at that site. Trapping was not carried out at Site 1 or Site 3 as evidence of bettong presence had ceased more than two weeks earlier. Any captured bettongs were individually marked with permanent marker at the base of their tail to allow subsequent identification on remote cameras.

Monitoring of bettong dispersal or mortality

Radio-collaring data obtained from a previous release outside Arid Recovery suggests that although some bettongs leave the release area, the majority (60%) remain within 5 km of their release location (Arid Recovery, unpubl. data; Moseby *et al.* 2011). In order to confirm that dispersal was not a significant cause of local population decline in the current study, spotlighting within the Release Zone and the wider Feral Control Area (up to 13 km from the Main Release Site) was undertaken approximately weekly to detect evidence of any dispersing bettongs while simultaneously conducting feral animal control. Additionally, in January 2014, after no bettongs were known to remain at the Main Release Site, a thorough search of the wider 500-km^2 Feral Control Area was conducted to determine whether bettong populations had established outside the Main Release Site. A total of 67 linear km of dunes were covered on foot and using an all-terrain vehicle within 5 km of release locations. Additionally, searches for bettong carcasses were undertaken a minimum of twice per week by searching across various dunes and swales within the Release Zone for evidence of bettong mortalities for four months after the initial bettong release. A minimum of 115 h of carcass searching was conducted, and the presence and location of bettong spoor found away from release sites was also recorded during searches. The stomach contents of all feral predators killed during feral control activities were examined for the presence of bettong remains.

Data analysis

To assess whether bettong, rabbit and predator detections differed between feeder and control sites, where 10 plots had been monitored per site over three sampling periods, binomial generalised linear models (GLMs) were developed (McCullagh 1983) with logit link functions using the program R, ver. 3.0.1 (R Development Core Team 2008). As each monitoring session was conducted on the same plots and only four days apart, replicates were not considered spatially or temporally independent and hence were analysed separately. A site dummy variable was not significant and was not included in the model. Treatment (feeder or control) was considered the explanatory

factor. Replicate 1 showed overdispersion and so was modelled using a quasibinomial GLM. Each model was then analysed for significant differences in plot activity between treatments (food and control) using a Chi-square test (Pearson 1900). These methods were repeated for the presence of dingoes, cats and rabbits. No foxes were recorded in any plots.

Results

Predator swamping

There was no difference in the persistence of bettongs released in large (Main Release Site) or small (Sites 1–3) groups, with no bettongs detectable at any release site four months after the initial release. At the Main Release Site, some bettongs persisted at feeders for between 42 and 122 days, while bettongs at Sites 1–3 persisted at feeders for between 2 and 41–53 days, with the exact time unknown due to a supplemental release 12 days after the first release at that site. As releases at the Main Release Site occurred over a four-month period, the exact longevity of individual bettongs could not be calculated. However, no bettongs were detected at the Main Release Site 42 days after the last release. Remote cameras at supplementary feeders captured natural behaviours including mating and the collection of nesting material a maximum of 18 days and 37 days after release respectively.

Twenty-one bettong carcasses or partial carcasses (1.7% of released bettongs) were located at the Main Release Site between July and October 2013. Post-mortem analysis of one carcass identified the likely cause of death as 'blunt toothed predation' by a dingo (Smith 2013). Cause of death was not determined for the remaining 20 carcasses, although predation was suspected for at least seven of these deaths. No carcasses were located at any of the three smaller release sites (Sites 1–3), although it is possible that carcasses may have been cached or fully consumed and therefore difficult to locate. No evidence of bettong remains was found in the stomachs of any cats or foxes shot in the Feral Control Area. Despite 428 h of spotlight searching, 145 h of foot or all-terrain vehicle searching and opportunistic monitoring methods surrounding release sites, only 16 records were made of bettongs that had dispersed outside the Main Release Site, either through track identification ($n = 12$), spotlighting of a live bettong ($n = 2$) or by cameras monitoring supplementary feeders positioned 500 m outside the Main Release Site ($n = 2$). At the Main Release Site, dingo track counts increased as bettong track counts increased; no changes in track counts for cats or foxes were observed over the study period (Fig. 2).

Supplementary feeding

There were significantly more bettong tracks present at feeder sites than at control sites (χ^2 test, $P < 0.001$, d.f. = 98, Replicate 1, 2 and 3) at the Main Release Site when sampling occurred in October 2013, one week after a supplemental bettong release (Fig. 3). The mean probability of finding bettong tracks in a plot at a feeder site was 0.64 (± 0.083) and at a control site was 0.03 (± 0.024). The presence of rabbit and cat tracks did not differ significantly between feeder and control sites for any session (χ^2 test, $P > 0.05$, d.f. = 98, Replicate 1, 2 and 3 for both species). No foxes were detected in any plots at any site during this experiment. The presence of dingoes at feeder and control plots was
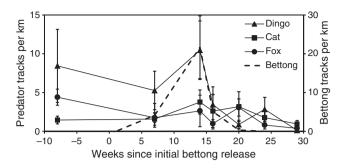
Fig. 2. Mean (±s.e.) number of tracks per kilometre for bettongs (secondary *y*-axis) and three mammalian predators (primary *y*-axis), based on the five transects (three dune, two vehicle) located within the Main Release Site.
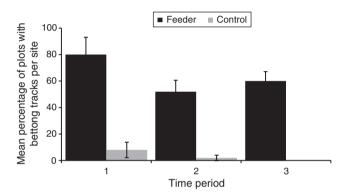

Fig. 3. Mean (±s.e.) percentage of sand plots with bettong tracks at feeder sites (*n* = 5) and control sites 200 m away from feeders (*n* = 5) within the Main Release Site. Tracks could be present in a maximum of 10 plots per site. The experiment was replicated over three periods, four days apart, using the same plots each time.

Fig. 4. The persistence (site fidelity) of bettongs at sites with (Sites 1 and 2) and without (Site 3) supplementary food, determined by remote cameras monitoring supplementary feeder structures.

inconsistent, with significantly more plots with dingo tracks at control sites than feeder sites during Replicate 1 (χ^2 test, $P = 0.017$, d.f. = 98) and significantly more dingo tracks found at feeder sites than control sites during Replicate 2 (χ^2 test, $P = 0.0073$, d.f. = 98). Dingo track counts did not significantly differ between treatments for Replicate 3 (χ^2 test, $P = 0.13$, d.f. = 98). As there was no evidence of any remaining bettongs after four months, we were unable to assess any long-term influence of supplementary feeding on body condition and reproduction. At the three smaller release sites (Sites 1–3), bettongs disappeared fastest from the site where no supplementary food was provided, with bettongs recorded in the area for only two days after release (Fig. 4). Bettongs at the two sites with food persisted at feeders for between 10 and 53 days. Site 1 (food) and Site 3 (no food) had a higher number of predator tracks on transects the first week after release than did Site 2 (food), where bettongs persisted longer. During the three weeks that five supplementary feeders were deployed 500 m outside the Main Release Site, feral cats were the only predators detected (on two nights), while during the same period inside the Main Release Site dingoes were detected at feeders on 10 nights and feral cats were detected on two nights.

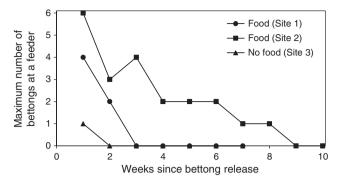One male bettong was trapped one month after release at a site with food (Site 2) and had lost weight (122 g, 6.7% of

prerelease body mass) and body condition. Eleven days after the bettong was trapped, a remote camera image was triggered by a feral cat entering the warren in which the bettong (with a tail marking) was observed to have entered the previous night and the bettong was not detected after that date. No predation events were recorded on remote camera, despite instances of bettongs and predators visiting the same feeder just hours apart. No bettongs were captured during the two nights of cage trapping at the Main Release Site in November.

Competition

Warren occupancy by rabbits increased by up to 25% in the six months following the initial bettong release; however, track counts for the species increased but then returned to baseline levels during the same period. Bettongs and rabbits were observed to regularly cohabit warrens, despite the ongoing vacancy of other warrens within the same area (Fig. 5). Rabbits were detected at feeders on 15.1% (±6.1) of nights while bettongs were detected at feeders on 72.8% (±7.4) of nights between July and November 2013, when bettongs were present in the area.

Discussion

Bettongs did not persist outside the Arid Recovery Reserve for more than four months, failing to establish at any of the four release sites. Releasing a large number of bettongs and providing supplementary food did not facilitate successful establishment of a free-ranging bettong population, although site fidelity was higher when supplementary food was provided. Previous mammal reintroductions have failed due to predation (Christensen and Burrows 1995; Moseby *et al*. 2011), stress (Dickens *et al*. 2010), hyperdispersal (Villaseñor *et al*. 2013) and disease (Thorne and Williams 1988). We discuss the validity of these explanations for this failed reintroduction.

Predation

Body parts/carcasses found at release sites with evidence of predation suggest that predation was one possible cause of the failure of this reintroduction, as had been recorded in previous failed reintroductions of this (Christensen and Burrows 1995; Short and Turner 2000; Moseby *et al*. 2011) and other related bettong species (Bellchambers 2001; Priddel and Wheeler
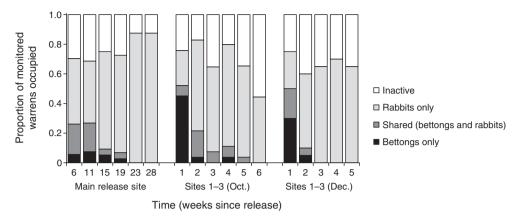
Fig. 5. The proportion of warrens occupied by bettongs and/or rabbits at the Main Release Site and Sites 1–3. Note that separate releases occurred at Sites 1–3 in October and December.

2004). Previous bettong releases that used tracking devices to monitor mortality revealed that predators were the biggest threat to reintroduction success (Short and Turner 2000; Moseby *et al.* 2011) and identified feral cats (Christensen and Burrows 1995; Moseby *et al.* 2011) and foxes (Short *et al.* 2002) as the main causes of predation; however, dingoes are also known to have undertaken surplus killing on a population immediately after release (Moseby *et al.* 2011). Despite previous studies suggesting that dingoes may provide protection for native mammals through suppression of mesopredators (Ritchie and Johnson 2009; Moseby *et al.* 2012), we found no evidence that releasing bettongs where dingoes were present facilitated a successful reintroduction. Predator numbers may have increased during the study as track counts for dingoes increased soon after the initial release and young dingoes were observed during this time on remote cameras. Dingoes were present at feeders inside the Main Release Area on more nights (*n* = 10) than they were outside the Main Release Area (*n* = 0) during a three-week period, suggesting that their localised distribution may have been influenced by the presence of bettongs. All three mammalian predators present at release sites are known to prey on burrowing bettongs (Christensen and Burrows 1995; Short *et al.* 2002; Moseby *et al.* 2011). As predation is the primary cause of reintroduction failure in Australia (Short *et al.* 1992; Fischer and Lindenmayer 2000; Short 2009), with the evidence we have collected we suggest that this was the most likely cause of this failed reintroduction.

Dispersal

With a high density of bettongs at the Main Release Site, it was expected that some, particularly males (Parsons *et al.* 2002), would naturally disperse, yet despite regular intensive predator spotlighting, track searches and remote camera monitoring only a small number (*n* = 16) of bettong sightings and spoor were observed outside the Main Release Site immediately after the release of almost 1000 bettongs, suggesting limited successful dispersal. Opportunistic observations made by five remote cameras (three with supplementary food provided) set up 500 m away from the Main Release Site for three weeks after the initial release detected just two bettongs, despite a supplemental release of bettongs occurring during this time. The failure to

detect more than two bettongs at these feeders during a time when dispersal was expected suggests limited successful movement away from the Main Release Site, particularly given the attraction of bettongs to feeders within the Main Release Site. While large dispersal distances have been recorded for some individual bettongs in previous releases (Short and Turner 2000; Moseby *et al.* 2011), most animals stayed close to their release site, and in this study we found no evidence to suggest that large numbers of bettongs had left release sites. In the absence of evidence of mass dispersal away from release sites, several explanations for significant bettong decline at release sites, other than predation, remain possible but unlikely.

Competition

Bettongs interacted with rabbits as both bettongs and rabbits used warrens and feeders. Yet despite rabbits and bettongs sharing warrens, vacant warrens in nearby areas suggests that warren availability or competition with rabbits for warrens was not a limiting factor for the reintroduction. A previous bettong release outside Arid Recovery recorded bettongs living in active rabbit warrens for up to four months after release (Moseby *et al.* 2011). Bettong detections at feeders far exceeded that of rabbits, suggesting that rabbits did not outcompete bettongs for supplementary food. Dietary overlap between the two species is low enough that competition is unlikely to have caused widespread bettong declines, especially at the rapid rate we observed (Robley *et al.* 2001). In other studies, increases in rabbit numbers have been shown to have no effect on bettong numbers, even in summer (Robley *et al.* 2002), so competition with rabbits is unlikely to explain this failed reintroduction.

Stress

Stress has not been reported as a critical factor in previous burrowing bettong translocations (Christensen and Burrows 1995; Short and Turner 2000; Moseby *et al.* 2011). While stress is an unavoidable component of all translocations (Teixeira *et al.* 2007; Dickens *et al.* 2010), we believe that the observation of bettongs exhibiting natural behaviours such as mating and collecting nesting material demonstrates that stress alone is unlikely to have caused reintroduction failure. While pouch

young of other bettong species have been lost after translocation (Priddel and Wheeler 2004), remote cameras showed that many bettongs at our sites had retained pouch young several weeks after release, suggesting that the translocation caused minimal stress. If stress was a leading cause of this failed reintroduction we would have expected to see significant declines in bettong numbers in the first few days after release rather than the weeks or months observed. By translocating bettongs in social and/or familial groups we aimed to limit the effects of stress after release.

Health

Disease is able to quickly reduce a population (Thompson *et al.* 2010) and translocating animals in suboptimal health has been known to influence reintroduction success (Thorne and Williams 1988; Priddel and Wheeler 2004; Mathews *et al.* 2006; Kingsley *et al.* 2012). Our local source population came from within the fenced Arid Recovery Reserve less than 20 km from the Main Release Site, in similar habitats. The source population showed no rapid decline or evidence of disease during the period preceding or following the translocation, so we believe disease is unlikely to have played a role in the failed reintroduction. Translocated animals were in optimal condition, with excellent body condition and no detectable ectoparasites. No evidence of illness was shown by bettongs on remote cameras and no abnormal behaviours such as being diurnally active were observed. If bettongs became totally reliant on supplementary food (rolled oats) it is possible that nutrient deficiencies may have compromised their health; however, we suggest this is unlikely to account for the decline of such a large number of animals, particularly as natural vegetation was considered to be in good condition at the time of the release.

Attempts to improve reintroduction success

The failure of bettongs to persist in the Release Zone following the reintroductions undertaken shows that the techniques we implemented to improve reintroduction success were unsuccessful. Bettongs released as part of a large release group did not persist and longevity was comparable to the persistence of bettongs at Site 2, where only 56 bettongs were released; therefore, predator swamping did not enhance the reintroduction success of burrowing bettongs. We acknowledge that the distance between release sites (4 km) was probably insufficient for the smaller release sites to act as effective control sites due to the large home range of dingoes, cats and foxes (Corbett 1995; Burrows *et al.* 2003); however, we do not believe that bettongs moved between release sites. There is little literature citing the use of predator swamping in a reintroduction context (e.g. Gerber *et al.* 2003), probably because a large source population of threatened species is rarely available. While it is generally accepted that larger release sizes have a higher probability of reintroduction success than smaller release sizes (Griffith *et al.* 1989; Fischer and Lindenmayer 2000; Kingsley *et al.* 2012), our results do not support this. Successful macropod reintroductions have occurred for some species with small release sizes but these have generally occurred on islands or into predator-free sanctuaries (Short *et al.* 1992). Predator swamping has been demonstrated as an effective defence against unsustainable

predation in prey species such as house mice (*Mus domesticus*) and common voles (*Microtus arvalis*) (Sinclair *et al.* 1990; Salamolard *et al.* 2000), but does not appear to have been effective for burrowing bettongs, perhaps due to prey naivety or high predation rates from introduced and/or native predators.

The use of supplementary food encouraged site fidelity in bettongs after release, with bettongs at the Main Release Site persisting for longer at feeder sites than at areas away from feeders. In a reintroduction context, this may be particularly useful as a means of reducing post-release dispersal and containing animals within a predator- or feral-species-control zone (Terman 1999; Rickett *et al.* 2013). Increased site fidelity has been demonstrated in dormice (*Muscardinus avellanarius*), prairie voles (*Microtus ochrogaster*) and cotton rats (*Sigmodon hispidus*) that were provided supplementary food following translocation (Cole and Batzli 1978; Bright and Morris 1994; Doonan and Slade 1995). We did not find conclusive evidence of higher predator presence close to feeders, although our remote camera detections of dingoes suggest that we cannot rule this out. Other studies have found that supplementary food may lead to increased predation as predators learn to target feeders (e.g. Dunn and Tessaglia 1994). However, no predation of bettongs was observed at feeders monitored by remote cameras, despite instances of dingoes sitting next to feeders. Unfortunately, due to the failure of the reintroduction, no conclusions regarding the influence of supplementary feeding on body condition and reproduction could be made on the basis of the single male re-trapped.

Our study was limited by our inability to radio-collar bettongs due to financial and logistical constraints. Our assertions regarding predation are therefore limited by the small amount of evidence we have for this and should be interpreted accordingly. However, the cumulative evidence we have presented regarding predators in this study, combined with the results from previous bettong translocations, suggests that predation is likely to have impacted on this reintroduction. Although our reintroduction attempt was unsuccessful, it is important that both successful and failed reintroductions are documented so that practitioners can learn from past failures and ultimately improve reintroduction success rates (Griffith *et al.* 1989; Short *et al.* 1992). We have shown that large release sizes do not always ensure reintroduction success and suggest that future mammal translocation projects consider this. We suggest that future research should further investigate the effects of supplementary feeding in reintroductions. Research should continue to identify and test new and novel methods for improving reintroduction success for Australian mammals.

Acknowledgements

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