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1

2 **Abstract**

3 Understanding the conditions under which small native Australian mammals can persist in the
4 presence of introduced predators remains a key challenge to conservation ecologists. Bettong-
5 specific *one-way gates* were used at a predator-free reserve in South Australia to allow the burrowing
6 bettong (*Bettongia lesueur*) – a small potoroid, listed as ‘vulnerable’ nationally - to disperse out of the
7 reserve. We conducted a field experiment to explore the conditions affecting residence time of
8 bettongs that left the reserve. We monitored bettong and mammalian predator activity outside the
9 fence using track surveys across 18 sites over two seasons. We examined the effect of supplementary
10 feeding as a strategy for increasing residence time, as well as the influence of predator presence and
11 habitat quality, using linear mixed models. Bettong activity was positively associated with
12 supplementary feeding, midstorey vegetation cover and shelter availability. After gates were closed,
13 bettong activity near gates declined to almost zero the following weeks, likely either due to death
14 from predation or movement away from the sites. To a small extent, mammalian predators were more
15 likely to be present at sites with high bettong activity. Further research on conditions to support
16 persistence of burrowing bettongs and other small mammals, including understanding minimum
17 necessary predator control effort, is required before successful establishment of populations outside of
18 fences can occur.

19

20 **key words**

21 burrowing bettong, translocation, augmented feeding, invasive predator, reintroduction, threatened
22 mammal, feral cat, arid zone

23

24 **Introduction**

25

26 In Australia, 32 terrestrial mammals have become extinct since European settlement and a large
27 proportion of persisting mammal species occupy less than 20% of their former range (Short & Smith
28 1994; Woinarski *et al.* 2015; Waller *et al.* 2017). A disproportionate number of extinctions and
29 declines have occurred among ‘critical weight range’ (CWR) mammals, weighing 35 – 5,500 g
30 (Burbidge & McKenzie 1989). These species are particularly susceptible to predation by feral cats
31 (*Felis catus*) and European foxes (*Vulpes Vulpes*), and their loss has negatively impacted ecosystem
32 function (James & Eldridge 2007).

33

34 Conservation on islands or fenced reserves free of introduced mammalian predators is currently the
35 only option to protect several Australian CWR species and prevent further extinctions (Legge *et al.*
36 2018). Yet, while fenced reserves have produced insurance populations of 38 predator-susceptible
37 species, developing and maintaining reserves comes at a cost. Reserves are limited in area and
38 capacity to expand. Contained mammals lose predator avoidance instincts unless predators are also
39 introduced, or predator-avoidance behaviours are instilled through training (Blumstein *et al.* 2002;
40 West *et al.* 2018). Notably, there is also risk of overpopulation because populations may not regulate
41 within closed systems where the full guild of native predators are absent (Slotow *et al.* 2005; Moseby
42 *et al.* 2018a). Fences also inhibit the dispersal and movement of free-ranging animals outside the
43 reserve (Slotow *et al.* 2005; Hayward *et al.* 2014). These challenges within predator-free areas have
44 the potential to result in counterproductive outcomes for both conservation and animal welfare.

45 There are currently few solutions to minimising effects of overpopulation within predator-free
46 reserves. Culling is widely seen as socially unacceptable and counter to conservation goals (Moseby
47 *et al.* 2018a), options for translocation on the scale required may not be available, and regulation by
48 mammalian predators within fenced reserves is not yet fully established. Reintroducing threatened
49 mammals outside predator-free areas therefore is desirable as a solution to overpopulation, but more
50 importantly to establish viable, self-sustaining populations (IUCN 2012) and return species’
51 ecological functions to the landscape (James & Eldridge 2007). However, medium-sized mammal
52 reintroductions beyond fences in Australia have had mixed outcomes (Moseby *et al.* 2011). The major
53 challenge in reintroducing medium-sized mammals outside of predator-free areas is managing the
54 threat of predation by cats, foxes and potentially native species (e.g., dingoes *Canis dingo*) (Short *et*
55 *al.* 1992; Moseby *et al.* 2011; Hardman *et al.* 2016). Further research is required to determine whether
56 successful reintroductions are possible with additional management actions (Short *et al.* 1992;
57 Moseby 2011a).

58 Actions to promote survival after release from a fenced sanctuary could include increasing predator
59 control, improving habitat conditions (including increased provision of shelter) and soft-release
60 methods. In some circumstances, introduced predators such as feral cats and foxes can be controlled
61 through poison baiting, shooting and trapping (Algar *et al.* 2013); however, effectiveness of control
62 depends on environmental conditions, location, density of predators and reinvasion rate (Moseby
63 2011b; Christensen *et al.* 2013). Alternatively, soft-release methods can be used to increase the
64 chances of establishment (e.g. Bright & Morris 1994, Short & Turner 2000; Tuberville *et al.* 2005;
65 Mitchell *et al.* 2011), Soft-release methods such as the provision of supplementary food, shelter or
66 acclimatisation pens aim to reduce the negative effects of sudden release by enhancing site fidelity,
67 familiarising animals with release site food and shelter, and minimising stress and panic-dispersal in
68 early stages of reintroduction (Moseby *et al.* 2014). The provision of supplementary food and water
69 have been tested previously with varying results (e.g. Bright & Morris 1994; Rickett *et al.* 2013;
70 Bannister *et al.* 2016).

71 This study sought to test availability of shelter and supplementary food as measures for improving
72 reintroduction outcomes in a release of CWR mammals conducted to prevent poor conservation and
73 animal welfare outcomes from overpopulation within a fenced reserve.

74 Arid Recovery (hereafter 'AR') is an ecosystem restoration initiative comprising a 123 km² reserve.
75 Burrowing bettongs (hereafter 'bettongs'), which formerly persisted across a large proportion of
76 southern Australia are now listed as 'vulnerable' nationally after having become extinct on the
77 mainland (Department of Environment, 2019). Bettongs were reintroduced to a predator-free section
78 of AR Reserve in 1999 (Moseby *et al.* 2011), and within ten years became overabundant (Moseby *et al.*
79 *al.* 2018a). The overabundance has negatively impacted vegetation, with likely flow-on negative
80 impacts to the population of greater stick-nest rats (*Leporillus conditor*) in the reserve, which rely on
81 the same food resources as bettongs (Linley *et al.* 2017; Moseby *et al.* 2018a).

82 A strategy tested at AR is bettong-specific one-way gates: small rectangular walk-ways with a vertical
83 Perspex flap allowing animals to push their way out of the fence (Crisp & Moseby 2010). The current
84 model of one-way gates has proven effective in allowing bettongs to disperse outside the fence, with
85 very low rates of non-target species using the gates and no incursions of introduced species (Butler *et al.*
86 *al.* 2018).

87 Bettongs' social behaviour and use of central warrens make them highly vulnerable to predation by
88 introduced species such as cats and foxes (Christensen & Burrows 1994). There have been two trials
89 to reintroduce bettongs from AR into unfenced, predator-controlled areas. Both were ultimately
90 unsuccessful, mainly due to predation, but also the rapid dispersal of released animals and/or drought
91 conditions (Moseby *et al.* 2011; Bannister *et al.* 2016), although there was some evidence that

92 supplementary feeding improved short-term survival of bettongs close to feeders (Bannister *et al.*
93 2016). In contrast, in an experiment within a fenced section of AR, a population of bettongs has been
94 able to establish and breed while co-existing with a controlled number of feral cats over a four year
95 period (Moseby *et al.* 2018b).

96 The release of bettongs through one-way gates at AR during 2017 and 2018 provided an opportunity
97 to build on learnings from the two previous bettong reintroductions to sites beyond the fence at AR.
98 Following a study by Bannister *et al.* (2016), which detailed poor survival of translocated bettongs,
99 our study aimed to clarify the potential of supplementary feeding to enhance bettong residence time
100 on dunes outside the AR fence close to one-way gates, and investigate how the presence of predators
101 and variation in habitat influenced the residence time. The experiment was designed to add value to
102 AR's bettong management program, which uses one-way gates to facilitate dispersal outside the
103 reserve. The results are expected to inform future outside-of-fence reintroductions of the species. We
104 predicted that bettong activity outside the fence would be high at one-way gate sites (and decline less
105 rapidly over time) where: (i) greater numbers of bettongs dispersed through one-way gates, (ii)
106 supplementary food was provided and (iii) vegetation cover and shelter availability were high. We
107 predicted that predators would be attracted to the bettongs and so would be more likely to occur at
108 sites where more bettong tracks were recorded.

109 **Methods**

110 *Study area*

111 The study took place at AR (30°29'S, 136°53'E), 20 km north of Roxby Downs, South Australia.
112 Feral cats, red foxes, dingoes and European rabbits (*Oryctolagus cuniculus*) are excluded from a 60
113 km² area within the reserve (Moseby and Read, 2006). Burrowing bettongs were the second species -
114 after greater stick nest rats – to be reintroduced to the reserve in 1999 (Finlayson & Moseby 2004).
115 Other species reintroduced are the greater bilby (*Macrotis lagotis*), western barred bandicoot
116 (*Perameles bougainville*) and recently, western quoll (*Dasyurus geoffroii*).

117 The landscape is dominated by east-west trending dunes with a sparse cover of tall shrubs and trees
118 including wattle (*Acacia ligulata*), hopbush (*Dodonaea viscosa*), mulga (*Acacia aneura*) and native
119 pine (*Callitris glaucophylla*), separated by inter-dunal swales dominated by low chenopods: saltbush
120 (*Atriplex vesicaria*) and bluebush (*Maireana astroticha*). Ephemeral canegrass (*Eragrostis*
121 *australasica*) swamp habitat is also found on the East boundary and open claypans on the West
122 boundary of AR. The climate is hot and dry with an average summer maximum temperature of 38°C,
123 average winter minimum temperature of 4°C and average rainfall of 143 mm per year (Bureau of
124 Meteorology 2019). A hot summer with below average rainfall led to drought conditions at AR in
125 2018 (Bureau of Meteorology 2019).

126 *Study species*

127 The bettong is a CWR mammal (average weight 1300g, height 500 – 700 mm) in the Potoroidae
128 family (Short & Turner 2000). Bettongs formerly lived across a large proportion of western and
129 southern mainland Australia but are currently confined to three natural populations on islands off the
130 coast of Western Australia, and translocated populations at AR in South Australia, Scotia Sanctuary in
131 New South Wales and Yookamurra Sanctuary in South Australia and Faure Island in Western
132 Australia (Woinarski *et al.* 2015; Kanowski *et al.* 2018).

133 Bettongs are nocturnal, feeding on shrub roots, stems, leaves, bulbs, insects and fungi (Bice &
134 Moseby 2008). They function as ‘ecological engineers’ as their digging and foraging promotes
135 nutrient enrichment for understory plants (Noble *et al.* 2007; James *et al.* 2009; Chapman 2015).

136 *Experimental Design*

137 We collected field data in two survey seasons: Spring 2017 and Autumn 2018.

138 Study sites were split along the West boundary and East boundary of the reserve (Fig. 1a). Gates were
139 installed on the Western and Eastern boundaries of the reserve, due to the location of habitat outside
140 the reserve, and the high abundance of bettongs in these areas. All gates were south of the dingo fence
141 where dingoes are controlled. However, the close proximity to the dingo fence (< 10km) meant that
142 some dingoes were present in the study area. Gates on the Western boundary were installed prior to
143 the commencement of this study in 2016 and gates on the Eastern boundary installed in 2017. Due to
144 East-West trending dunes, the location of gates also allowed monitoring of animal tracks to be within
145 a similar distance from the fence across sites. In 2017, we monitored 11 sites on the West boundary
146 and seven on the East boundary. In 2018, we monitored nine of the 11 sites on the West boundary and
147 all seven East boundary sites.

148

149 Each site comprised a one-way gate and an associated east-west dune running approximately
150 perpendicular to the AR fence (Fig. 1b). At each West boundary site, we monitored bettong and
151 predator tracks along a 300-m transect along the ridge of the dune closest to the one-way gate –
152 starting five metres from the fence. On the East boundary, transect lengths varied from 80 - 300 m
153 (mean length 270 m) because dune habitat at some sites rapidly transitioned to salt bush swale or
154 ephemeral canegrass swamp, making it difficult to observe animal tracks. Sites were 300 – 1000 m
155 apart.

156 In each season, we provided supplementary food at ten sites (of 18 surveyed in 2017 and of 16
157 surveyed in 2018), including sites on the East and West boundaries. We placed feeders 100 m from
158 one-way gates and within 50 m of track transects underneath tall shrubs. Feeders comprised a 50 cm

159 long PVC pipe (diameter = 10 cm) fixed above a 20 cm diameter plastic feeding tray and attached by
160 wire to two two-metre pickets hammered into the soil. During the treatment stage we ensured feeders
161 contained 1500 g of feed (rolled oats) each evening.

162 In each season, we monitored sites across two phases (Fig. 1c):

- 163 • Phase 1. This ‘gates open’ phase comprised firstly a non-feeding stage where one-way gates
164 were open, but no supplementary food was provided outside the gates (two weeks in 2017;
165 one week in 2018), followed by a treatment stage when supplementary feeding (hereafter
166 ‘feeding’) was introduced to feeding sites (four weeks in 2017; two weeks – East boundary,
167 and one week – West boundary 2018). This phase allowed a baseline to be established for the
168 bettong track counts at each site before one-way gates were closed.
- 169 • Phase 2 (‘gates closed’ phase) comprised closing one-way gates and continued feeding at
170 feeding sites for the remainder of the season (three weeks in 2017; five weeks – East
171 boundary, and three weeks – West boundary 2018).

172 We extended Phase 2 in 2018 to extend monitoring of bettong residence time for an extra two weeks

Figure 1. (a) Locations of one-way gate sites on the East and West boundaries of Arid Recovery, South Australia. (b) Magnified view of site 15 on the East boundary. (c) Survey timeline for 2017 and 2018 seasons. The experiment was conducted in two Phases. Phase 1 included a period of monitoring in which one-way gates were open and food placed daily – including an initial non-feeding stage at all sites (yellow) and an experimental treatment stage where supplementary feeding was introduced at feeding sites (green). Phase 2 involved a period of monitoring in which one-way gates were closed and treatments continued (orange).

173 after closing gates. The lengths of monitoring stages were varied between the East and West
174 boundaries in 2018 to accommodate essential fence maintenance works on the eastern boundary at the
175 start of this survey season. One-way gates monitoring

176 We checked open one-way gates daily and put ~20g of peanut butter outside the gates to attract
177 bettongs through the gates. We used camera-traps to determine the number of individuals moving
178 through one-way gates. One-way gates were open for 41 nights each on the West and East boundaries
179 in 2017, and 12 nights on the West boundary and 22 nights on East boundary in 2018 (Fig. 1c). We
180 deployed two *Reconyx HC600* cameras at each gate while gates were open, one camera facing the
181 inside part of the gate, and one facing the exit point, with the following settings: high sensitivity,
182 *RapidFire*, no delay between triggers, one image per trigger (Butler *et al.* 2018).

183 We separated exit images from non-exit images by comparing inside and outside camera trap images.
184 An exit was determined by an image of a bettong entering a gate followed by an image of the bettong
185 outside of the fence within 1 minute (Fig. A1.1 Supp. mat). An exit was only counted if the inside and
186 outside cameras were triggered. We collated exit images and recorded the number of exits through
187 each gate on each night.

188 *Track monitoring*

189 The afternoon prior to surveying transects, we smoothed a track along the dune at each site by
190 dragging a one-metre-wide rubber mat with rope along the length of the transect (Fig. A1.2). We
191 surveyed transects between one and three hours after sunrise the following morning to allow good
192 visibility of tracks. We recorded the number of bettong tracks – counting one track each time an
193 animal crossed onto and off the transect (Moseby *et al.* 2011). Predators (cats, foxes and dingoes)
194 were recorded as present or absent for each transect (Table A2.3).

195 We repeated each transect survey every three to four days throughout the survey seasons. All transects
196 were surveyed 15 times in 2017; East boundary transects were surveyed 19 times and West boundary
197 transects 10 times in 2018.

198 *Habitat surveys*

199 At each site, we surveyed vegetation along two perpendicular 100-m line transects, centred on the
200 dune 100 m from the start of the track transect (Fig. 1b). We used a ‘touchpole’ method to record the
201 presence of vegetation contacting a 1.5-m pole in two height classes: ‘midstorey’ (0.3 – 1.5 m) and
202 ‘canopy’ (>1.5 m) (adapted from D’Antonio *et al.* 2011). The method involves placing a pole
203 marked at fixed heights along a transect and recording vegetation presence or absence (or vegetation
204 type or species) at the heights of interest. Midstorey vegetation was considered to indicate potential
205 protection from terrestrial predators, while canopy vegetation potentially indicated protection from
206 aerial predators. Touches were recorded at 0.5 m intervals along each line transect (400 points in
207 total). We then calculated the percentage of touches for each height class, derived the median, and
208 categorised the vegetation cover as ‘low’ (less than the median; 10.5% for midstorey vegetation and
209 2.75% for canopy vegetation) or ‘high’ (equal to or greater than the median).

210 We recorded available shelter at each site by counting rabbit warrens for 300-m along each dune on
211 which track surveys were conducted (Table A2.2). To ensure the entire width of the dune was
212 searched, three people walked along the dune together 30 – 50 m apart and marked warren locations
213 with a *Garmin etrex 10* GPS. Warrens of any number of entrances (usually between two and five) and
214 warrens appearing to be actively or recently used by rabbits were considered. There were no warrens
215 observed in the swale habitat between dune study sites.

216 *Predator control*

217 Cat and fox control occurred outside the fence before and during both field seasons out to a buffer of
218 10 km from the reserve, including trapping, poison baiting at 5 baits/km of track, and spotlight
219 shooting. Nineteen cats and one fox were removed on 14 shooting nights before and during the Spring
220 2017 field season, and 100 poison (0.04 g/kg sodium fluoroacetate ‘1080’) semi-dried kangaroo meat
221 baits were distributed by hand on vehicle tracks within five km of the perimeter in August 2017.

222 Before and during the Autumn 2018 field season, five cats and one fox were killed on six shooting
223 nights. Eight hundred semi-dried kangaroo meat baits were laid in March and April 2018 in a larger
224 buffer up to 10 km around the reserve. Nineteen cats were caught in foothold and cage traps set
225 around the reserve on 297 trap nights within two weeks prior to the Autumn 2018 field season.

226 *Statistical analysis*

227 Bettong activity

228 To test our predictions about the drivers of bettong residence time, we characterised the relationship
229 between bettong track count after the gates were closed (Phase 2) and the independent variables listed
230 in Table 1 using generalised linear mixed models with a Poisson link function, appropriate when the
231 dependent variable is a count. Models were fitted in R v3.3.3 (R Core Team 2013) using package
232 *lme4* (Bates *et al.* 2014). We standardised continuous independent variables by dividing raw data
233 values by maximum values. A random intercept structure was included to account for the nestedness
234 of the survey design (repeat surveys of sites grouped along East and West boundaries within each
235 survey season) (Table 1). An observation-level random effect was also included to account for
236 overdispersion of count data cf. the Poisson distribution; equivalent to a Poisson log-normal
237 observation model (Harrison 2014). To meet the model assumptions of homogeneity of residuals it
238 was necessary to include an interaction term between the season (2017 vs. 2018) and side (east vs.
239 west), and to include a quadratic term for the effect of day since gate opening on track counts.

240 Predator occurrence

241 To test our *a priori* hypotheses about drivers of predator occurrence, we characterised the relationship
242 between predator presence throughout the monitoring period, including after gates were opened
243 (Phases 1 and 2) and the independent variables listed in Table 1, using generalised linear mixed
244 models with binomial error distributions and a logit-link function, appropriate when the dependent
245 variable is binary. We determined predator presence by the presence of cat, fox and/or dingo tracks on
246 a transect. Again, a random intercept structure was included to account for the nestedness of the
247 survey design. Presence of cat, fox and dingo tracks were analysed together.

248 Model selection

249 For each set of predictions, we used function *dredge* in R package *MuMIn* (Barton 2013) to compare
250 the best model subsets of the full model set (Table A3.1). In the bettong activity model we always
251 retained random effects and the season/side interaction in the subset models. We also allowed fitting
252 of two-way interactions of interest, for example an interaction term for days and feeding treatment.
253 The null models for bettong activity and predator occurrence comprised only the random effects and
254 season/side interaction as predictor variables. For both models, variable selection was based on
255 Akaike's Information Criterion adjusted for small sample size (AICc) which measures performance

256 based on a trade-off between model fit and model complexity (Akaike 1973; Cavanaugh 1997). The
257 top-ranked bettong activity model included all variables in the top dredged models (>2 AICc of the
258 first model), with the observation-level random effect. We used the top-ranked bettong activity and
259 predator occurrence models to create fitted response plots of individual predictors.

260 We ensured that top-ranked models met statistical regression modelling assumptions of homogenous,
261 independent, and appropriately-dispersed residuals by analysing randomised quantile residuals with
262 the R package *DHARma* (Hartig 2018), visual checks, simulation tests, and Durbin-Watson tests for
263 temporal autocorrelation (Fig A3.1; A3.2; A3.3).

264 **Results**

265 *Bettongs*

266 In total, we recorded 1223 bettongs exits through the one-way gates in spring 2017 and 349 bettongs
267 exits in autumn 2018. Average exits per gate per night were 0.93 on the West and 2.69 on the East in
268 2017, and 0.38 per gate per night on the West and 2.37 on the East in 2018 (Table A2.1). No bettongs
269 were observed regaining access to the reserve through the one-way gates once they had exited.

270 In both survey seasons, the number of bettong tracks on transects increased immediately after gates
271 were opened but started to decline at some sites before gates were closed. Tracks declined after one-
272 way gates were closed, particularly in 2018 (Fig. A2.3; Fig. 2). There was strong consistency among
273 the six top-ranked models of bettong activity (track count) after gates were closed (Table 2). The fixed
274 effects of each of the six models explained approximately 90% of the variation in track counts (Table
275 2). The number of bettong tracks was substantially higher at sites where food was provided and lower
276 at sites where predators were present (Table 2; Fig. 2; Fig. 3a). The interaction between food and
277 predator presence had a positive effect on daily track counts which reinforces that predators tended to
278 be attracted to sites of high bettong activity (Table 2; Fig. 3a). Shelter availability was strongly
279 positively associated with daily track counts (Table 2; Fig. 3a), and mid-storey shrub cover and
280 canopy vegetation cover were weakly positively associated with daily track count (Table 2; Fig. 3a).
281 At all sites, the daily count of bettong tracks declined with time since gate closure (Table 2; Fig. 2).
282 Where food was provided, the number of tracks declined more rapidly (Fig. 2). In summary, while
283 food increased initial bettong activity, the number of tracks at sites with high initial bettong activity
284 (feeding sites) tended decline fastest. The association between high activity sites and predator
285 presence provides some support to the hypothesis that predators, rather than dispersal were the main
286 agents of decline following gate closure, and that high bettong activity tends to attract predators in.

287 *Predators*

288 Despite the effort to control predators prior to opening one-way gates, feral cats and foxes persisted in
289 the area. Trapping rates of feral cats along the fence line were particularly high prior to gates opening

290 in 2018 (19 cats caught in two weeks). We recorded predator tracks in 81% of transect surveys in
291 2017 compared to 67% in 2018. Feral cats predominated, with relatively few records of foxes and
292 dingoes (Table 3). While conducting track surveys, we found evidence of wedge-tailed eagles (*Aquila*
293 *audax*), feral cats and dingoes preying or scavenging on bettongs. In Spring 2017, 33 bettong
294 carcasses were found nearby the East boundary and three nearby the West boundary. In Autumn 2018,
295 24 bettong carcasses were found on the East boundary. Twice each, feral cats and dingos were
296 detected on camera traps by gates on the East boundary in 2018. Wedge-tailed eagles were observed
297 killing bettongs that had recently exited one-way gates and were yet to establish warrens. Once
298 warrens were established, the rate of wedge-tailed eagle predation appeared to decline. Feral cat
299 tracks were observed close to transects and showed evidence of bettong predation, including one
300 instance of a cat predating a bettong close to a feeder.

301 Our top-ranked model of predator presence over the entire monitoring period (i.e. while gates were
302 open and after they were closed), showed that survey season (2017/2018) had the strongest effect,
303 with predators more likely to be detected in 2018 than 2017 (Table 2; Fig. 3b; Fig. 4). To a small
304 extent, predators were also more likely to be recorded as the number of bettong tracks increased (Fig.
305 4), averaging 70% presence on any given transect when bettongs were abundant. Supplementary food
306 was not selected in the top-ranked predator presence model, however, the positive relationship
307 between feeding and bettongs and the positive relationship between bettongs and predators indicates
308 that anything that creates a high bettong density, including feeding will likely attract predators.

309 **Figure 2: Fitted response plots for variables included in top-ranked bettong activity model, showing the response of**
310 **bettong track counts per day per transect to food and predator presence in a), b), c) and d) 2017 and e), f), g) and h)**
311 **in 2018 at East boundary sites. Line shows mean of fitted response with 95% confidence limits shaded. Plotted points**
312 **are recorded values.**

313 **Figure 3: Ordered effect-size plot for the top-ranked (a) bettong activity model and (b) predator presence model. *day***
314 **– *day* since one-way gates closed in bettong activity model and *day* since gates first opened in the predator presence**
315 **model. The proportion of models the variable is included in out of six AICc top-ranked models is bracketed next to**
316 **each variable in a)**

317 **Figure 4: Fitted response plot for AIC-top-ranked model of predator presence, showing response of probability of**
318 **predator presence to bettong tracks per day per transect in Spring 2017 (solid) and Autumn 2018 (dotted line) survey**
319 **seasons.**

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Discussion

Reintroduction of threatened mammals beyond predator-free havens is important for their ongoing conservation (Short *et al.* 1992; Christensen & Burrows 1994). Yet, despite close to 1,600 bettongs exiting the one-way gates in our study, few remained at monitoring sites for longer than three months, with most disappearing within a month after gates were closed in either survey season. We located many bettong carcasses and signs of predation near one-way gates. After gates were closed, bettong track counts declined most rapidly when predators were present, indicating that mortality due to predators, rather than movement away from gate sites is likely to be responsible for the rapid decline in activity. Although bettongs did not persist for any substantial length of time on survey transects after gates were closed, we found that supplementary feeding, vegetation cover and shelter availability had a positive effect on bettong activity, as hypothesised, indicating that if predators could be reduced or removed, supplementary feeding would be a good approach to avoiding hyperdispersal and act as a form of soft release.

Supplementary feeding

Bettong track counts were higher at feeding sites compared with non-feeding sites, supporting the hypothesis that feeding encourages site fidelity which reinforces similar findings for other species such as prairie voles, dormice and cotton rats (Cole & Batzli 1978; Bright & Morris 1994; Doonan &

350 Slade 1995). However, counts declined more quickly at feeding sites, indicating feeding was not
351 associated with increased residence time. Supplementary food may have enabled bettongs to feed
352 more efficiently at night and so spend less time exposed to predators outside shelter and/or reduced
353 competitive pressure to disperse. However, it did not ultimately result in substantially better outcomes
354 for bettongs in the presence of high predator pressure.

355 While feeding had a positive effect on bettong site residence after gates were closed, the association
356 between high numbers of predators and areas with high bettong activity was concerning and indicates
357 a potential trade-off. While we did not explicitly test for it in our study, it is possible that predators
358 target feeding stations frequented by prey species (e.g. Dunn and Tessaglia-Hymes, 1994). Future
359 studies should seek to clarify whether feeders benefit prey persistence in the presence of predators and
360 under varying levels of predator control. Supplementary feeding accompanied by targeted predator
361 control around feeders may be an effective way to distribute predator control resources and increase
362 bettong residence time.

363 *Predation*

364 Bettong track counts were lower in surveys when predators (cats, foxes or dingoes) were present at
365 non-feeding sites but higher at feeding sites. Similarly, predators were more likely to be detected
366 when bettong track counts were high. This suggests that predators were associated with high levels of
367 bettong activity either because predators were attracted to the prey activity or because both bettongs
368 and predators are attracted to similar habitat attributes (e.g. rabbit warrens for shelter) (Moseby *et al.*
369 2009). Feral cats and foxes are known to travel long distances to access plentiful food resources
370 (Bubela *et al.* 1998; Tsukada 1997; McGregor *et al.* 2015). In our study, predator activity at sites was
371 not measured prior to the gates being open so we cannot categorically state that predators were
372 attracted to sites where bettong activity was high rather than being attracted to similar site attributes.
373 However, it would appear that the strong relationship between predator presence and bettong track
374 count indicates prey-tracking by predators is quite likely.

375 Evidence of predation at study sites (bettong carcasses) reinforces the primary role of predation in the
376 rapid demise of bettongs, in line with previous reintroduction studies (Christensen & Burrows 1994;
377 Short & Turner 2000; Moseby *et al.* 2011; Bannister *et al.*, 2016). We regularly found bettong
378 carcasses and remains near the fenceline with tracks and puncture wounds indicating predation by
379 wedge-tailed eagles, dingoes and cats. Most carcasses suspected to be killed by dingoes were largely
380 intact, consistent with the known hunting behaviour of dingoes on bettongs and their tendency to
381 surplus kill (Thomson 1992; Moseby *et al.* 2011). Predation by dingoes and wedge-tailed eagles
382 appeared to be highest immediately after bettongs exit gates, when animals had not yet established or
383 located burrows and were easier prey for predators that hunt using visual cues. Camera trap images of
384 cats and dingoes investigating one-way gates suggest the predators were aware of gates. We did not

385 observe any conclusive evidence of fox predation. Fox tracks were recorded less frequently than cat
386 and dog tracks, potentially due to their avoidance of dingoes at a fine spatial scale (Mitchell & Bank
387 2005; Moseby *et al.* 2012).

388 More intensive and sustained predator control should be tested in the future to determine if bettongs
389 can survive outside of the reserve when supportive measures such as feeding and supplementary
390 shelter are combined with intensive predator control. Aerial baiting was not conducted during our
391 study and despite ground baiting, shooting and trapping occurring around the perimeter of the reserve,
392 predator control was relatively localised. Previous attempts to use aerial baiting to control predators
393 around AR were unsuccessful at controlling cats but successfully controlled foxes (Moseby & Hill
394 2011). Intensive control could include aerial baiting for foxes, Felixer grooming traps and leghold
395 traps for feral cats and rabbit control to naturally reduce predator abundance. These activities could
396 occur within at least a 10 km radius of the reserve to reduce re-invasion rates. There is a precedent for
397 bettongs co-existing with low densities of cats - 0.46 cats per square km within a large enclosed area
398 (Moseby *et al.* 2018b). This density is higher than the estimated average density of feral cats across
399 Australia (0.27 cats per square km) (Legge *et al.* 2017). The role of dingoes in reintroduction of
400 critical-weight-range mammals also requires further research. While dingoes and bettongs co-existed
401 prior to European settlement, it is unclear how to manage dingoes at open-landscape reintroduction
402 sites given the evidence of dingo predation on bettongs from this study and others (Bannister *et al.*
403 2016). Improved understanding of co-existence thresholds for vulnerable native prey such as bettongs,
404 and the influence of other factors such as the availability of alternative prey, will guide efforts for
405 reintroductions outside of predator-free areas.

406 *Dispersal*

407 In addition to predation, dispersal may have been a factor in the relatively short residence time of
408 bettong sign on transects. Bettongs are social animals, and some individuals may have moved away
409 from gates due to hyperdispersal after being separated from their warren group (Kleiman 1989;
410 Thompson *et al.* 2001) or gradually dispersed to dunes further from their exit point as more bettongs
411 exited the gates and density increased (Moseby *et al.* 2011; West *et al.* 2018). The distance between
412 dunes was well within the home range radius of this species (Finlayson & Moseby 2004). However,
413 the positive correlation between bettong tracks and number of exits at nearby gates suggests that most
414 animals were not hyperdispersing but staying close to the point at which they exited the reserve, at
415 least initially.

416 Three times more bettongs dispersed through one-way gates in 2017 than in 2018, mainly due to gates
417 being open for a longer period (six weeks in 2017 compared to two weeks on the West boundary or
418 four weeks on the East boundary in 2018). Drier conditions likely influenced the behaviour of
419 bettongs inside and outside of the reserve, the vegetation cover available for use and bettongs'

420 reliance on supplementary food. The recent dry conditions also mean we will need to wait until
421 significant rains to test the effect of exit of 1600 bettongs from the reserve on vegetation recovery
422 within the reserve. Exit rates were slightly lower in 2018, likely because of previous exits by bettongs
423 with warrens close to one-way gates. Consistently higher rates of exits through gates on the East
424 boundary and higher local bettong activity were likely due to all gates on this side being newly
425 opened (gates on the west side had been in use previously), and the presence of free water from a
426 leaking pipeline outside the eastern fence. The effect of distance to free water is not explicitly
427 modelled here. Free water only existed outside the eastern fence, so its effect would be statistically
428 confounded by other differences between east and west sides of the reserve.

429 *Habitat*

430 As predicted, bettong activity was higher at sites with greater mid-storey and canopy vegetation
431 cover. Mid-storey cover is likely to protect bettongs from predators and/or provide food. However,
432 this effect was not statistically significant, potentially because there was low variation in shrub cover
433 across sites and low cover generally. Canopy cover was a weak predictor for bettong tracks and is
434 likely to be a less important resource for bettongs. Our hypothesis that bettong activity would be
435 higher at sites with more rabbit warrens was supported, reinforcing that shelter is a vitally important
436 resource for bettongs and the bettongs will use burrows constructed by rabbits (Robley et al. 2002).

437 *Management implications and future research*

438 Bettong track counts were higher and declined more quickly when food was provided. This suggests
439 that a higher number of individuals were supported at feeding sites and these animals dispersed or
440 were predated faster than at non-feeding sites. However, we were unable to directly test these
441 hypotheses as individual bettongs were not radio-collared.

442 This study reinforces understanding that supplementary feeding can enhance activity (and potentially
443 site fidelity) in reintroduced species but is unlikely to increase residence time in the absence of
444 intensive predator control (Rickett *et al.* 2013; Bannister *et al.* 2016; De Milliano *et al.* 2016). Re-
445 establishing self-sustaining populations of locally extinct species such as bettongs outside predator-
446 free areas may be possible if habitat requirements are met and sufficient predator control is applied,
447 however this remains challenging (Moseby *et al.* 2011). Future studies could use a stratified
448 experimental design to identify the interactions between feeding, habitat and minimum predator
449 thresholds. Quantifying predation rates close to and remote from feeders would assist in determining
450 the net benefit of soft-release feeding. Importantly, differentiating between mortality and bettong
451 dispersal away from one-way gate sites is essential and would require radio-collaring and close
452 monitoring of bettongs that exited gates.

453 Management of overabundant populations of threatened species within predator-free havens remains a
454 challenge. As yet, there is no evidence for density dependent reductions in reproductive rates for
455 burrowing bettongs (Finlayson & Moseby 2004), and it is clear that such population regulation is
456 insufficient to maintain the bettong population at a level that does not negatively impact vegetation
457 condition and other threatened species (Moseby et al. 2018). One-way gates facilitating dispersal out
458 of fenced reserves are effective at reducing the density of bettongs within the reserve (Arid Recovery,
459 unpublished data) but the difficulty of establishing dispersing animals outside the fence must be
460 considered in balancing conservation and animal welfare goals in managing confined populations. A
461 more sustainable option currently being tested may be regulation by introduction of native
462 mammalian predators (West et al. 2019).

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645 **Tables**

646 **Table 1: Summary of independent variables offered to the models. ‘*’ indicates the reference level for categorical**
647 **variables**

Predictor	Predictor type	Description
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Bettong activity		Sum of tracks on a transect for a given day
<i>day since gates closed</i>	Continuous	
<i>survey season</i>	Factor	Spring 2017*/Autumn 2018
<i>one-way gate exits</i>	Continuous	cumulative total exits
<i>feeding treatment</i>	Factor	non-feeding*/feeding treatment
<i>midstorey vegetation cover</i>	Factor	<i>low, high</i> , relative to median cover value for this height class (10.5%)
<i>canopy vegetation cover</i>	Factor	<i>low, high</i> , relative to median cover value for this height class (2.75%)
<i>shelter availability</i>	Continuous	number of warrens at a site
<i>predator presence</i>	Factor	daily absence*/presence of cat, fox and/or dingo tracks on survey transect
<i>site and East/West boundary</i>	Categorical	random intercept effect to account for the nestedness of the survey design (sites grouped along East and West boundaries, with repeat surveys of each site within each survey season)
Predator occurrence		
<i>bettong track count</i>	Continuous	
<i>survey season</i>	Factor	Spring 2017*/Autumn 2018
<i>treatment</i>	Categorical	non-feeding*/feeding treatment
<i>day since gates opened</i>	Continuous	
<i>site within East/West boundary</i>	Categorical	random intercept effect to account for the nestedness of the survey design (sites grouped along East and West boundaries, with repeat surveys of each site within each survey season)

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649 **Table 2: Top-ranked models ($\Delta AICc \leq 2$) of bettong activity and predator occurrence, relative to the null model.**
650 **Predictors are described in Table 1. ‘Top-ranked’ refers to the bettong activity model including all variables in the**
651 **top six dredged models. ‘*’ indicates a statistically significant relationship (< 0.05). *df* refers to model degrees of**
652 **freedom; *weight* to the probability that a given model is the best, relative to other models; R^2m the marginal R-**
653 **squared value (conditional on fixed variables); R^2c the conditional R-squared value (conditional on fixed and random**
654 **variables)**

Bettong Activity															
	<i>predator presence</i>	<i>shelter</i>	<i>total exits</i>	<i>food</i>	<i>canopy vegetation</i>	<i>shrub cover</i>	<i>day:predator presence</i>	<i>day:food</i>	<i>predator presence:food</i>	<i>df</i>	$\Delta AICc$	<i>weight</i>	R^2m	R^2c	
top-ranked	-0.69*	0.73*	0.13	0.84*	0.01	0.23	0.72	-0.45	0.59*	17			0.91	1.00	
1	-0.63*	0.89*		0.51*		0.16*			0.77*	13	0.00	0.12	0.90	1.00	

2	-0.63*	0.88*		0.47*		0.16*	0.19	0.77*	14	0.60	0.09	0.90	1.00
3	-0.64*	0.88*		0.51*	0.03	0.16*		0.78*	14	1.08	0.07	0.90	1.00
4	-0.66*	0.88*	-0.04	0.50*		0.15*		0.78*	14	1.66	0.05	0.90	1.00
5	-0.64*	0.88*		0.46*	0.03	0.16*	0.19	0.78*	15	1.69	0.05	0.90	1.00
6	-0.61*	0.89*		0.51*		0.16*	-0.10	0.77*	14	1.75	0.05	0.90	1.00
null									5	5353.87	0.00	0.81	1.00

Predator Occurrence

	<i>betting track count</i>	<i>day since gates opened</i>	<i>food</i>	<i>season</i>	<i>df</i>	$\Delta AICc$	<i>weight</i>	R^2m	R^2c
1	0*	0.04*		1.7*	6	0	0.52	0.17	0.35
2	0.01	0.04*	-0.26	1.76*	7	1.56	0.24	0.17	0.36
null					3	50.23	0	0	0.11

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658 **Table 3: Proportion of survey days predators were recorded on transects in Spring 2017 and Autumn 2018 and**
659 **averaged across both seasons at Arid Recovery Reserve, South Australia.**

Survey	all predators	cats	foxes	dingoes	N surveys
2017	0.67	0.63	0.10	0.10	144
2018	0.81	0.76	0.02	0.16	99
Average	0.74	0.70	0.06	0.13	

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