

Cats are a key threatening factor to the survival of local populations of native small mammals in Australia's tropical savannas

Evidence from translocation trials with *Rattus tunneyi*

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1 Cats are a key threatening factor to the survival of local populations of native
2 small mammals in Australia's tropical savannas: evidence from translocation
3 trials with *Rattus tunneyi*

4 **Short text for table of contents**

5 Feral cats are thought to be a key factor driving declines of small mammals in northern Australia.
6 However, evidence thus far remains circumstantial and correlative. In this trial, we tested survival of
7 pale field rats *Rattus tunneyi* when translocated into experimental enclosures where access by cats
8 was manipulated. Cats rapidly killed rats in cat-accessible enclosures, demonstrating that even at
9 low densities, feral cats can drive small mammal populations to extinction.

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35

36 **Abstract**

37 *Context*

38 Invasive predators are a key threat to biodiversity worldwide. In Australia, feral cats are likely

39 responsible for many extinctions of native mammal species in the south and centre of the continent.

40 *Aims*

41 Here we examine the effect of feral cats on native rodent populations in the second of two

42 translocation experiments.

43 *Methods*

44 In a wild-to-wild translocation, we introduced pale field rats, *Rattus tunneyi*, whose populations are
45 declining in the wild, into two pairs of enclosures where accessibility by feral cats was manipulated.

46 *Key results*

47 Individual rats translocated into enclosures accessible to cats were rapidly extirpated after cats were
48 first detected visiting the enclosures. Rats in the enclosure not exposed to cats were 6.2 times more
49 likely to survive than those exposed to cats. Two individual cats were responsible for the deaths of
50 all but one of 18 cat-accessible rats. Rats in the site with denser ground cover persisted better than
51 in the site with more open cover.

52 *Conclusions*

53 These results are consistent with our previous study of a different native rat species in the same
54 experimental setup, and provide further evidence that, even at low densities, feral cats can drive
55 local populations of small mammals to extinction.

56 *Implications*

57 Effective feral cat control may be necessary to enable recovery of small mammals.

58

59 **Keywords**

60 Feral cat, extinction, threatened species, predation pressure, small mammal populations

61

62 **Online summary**

63 Feral cats are thought to be a key factor driving declines of small mammals in northern Australia.
64 However, evidence thus far remains circumstantial and correlative. In this trial, we tested survival of
65 pale field rats *Rattus tunneyi* when translocated into experimental enclosures where access by cats
66 was manipulated. Cats rapidly killed rats in cat-accessible enclosures, demonstrating that even at
67 low densities, feral cats can drive small mammal populations to extinction.

68 **Introduction**

69 Introduced predators are a pervasive driver of extinction globally (Bellard *et al.*, 2016); they are
70 implicated in most contemporary extinctions (58%) of bird, mammal and reptile species (Bonnaud *et*
71 *al.*, 2012; Woinarski *et al.*, 2015; Doherty *et al.*, 2016), with particularly devastating effects on islands
72 (Medina *et al.*, 2011). Effects of predators are most severe when predation is depensatory, such that
73 the predation rate on individuals of the prey species increases as the population drops below a
74 certain threshold, with the result that prey fall into a predator sink (Pech *et al.*, 1995).

75 Predation by introduced cats (*Felis catus*) has caused extinctions and ongoing declines of many
76 mammal species in temperate, arid and semi-arid Australia, and is a key factor in the recent and
77 ongoing decline of many small mammal species across much of northern Australia (Fisher *et al.*,
78 2014; Lawes *et al.*, 2015; Ziembicki *et al.*, 2015). Several native mammal species have contracted to
79 cat-free islands or areas of rugged topography where the density of cats, or their hunting efficiency,
80 is low (Woinarski *et al.*, 2011; Hohnen *et al.*, 2016; Stobo-Wilson *et al.*, 2020), and all of the declining
81 species are within the size range of prey preferred by cats (Fisher *et al.*, 2014). However, the
82 evidence that predation by cats is a main cause of these declines in northern Australia remains
83 mostly correlative or circumstantial. Here we present direct evidence from a large-scale field
84 experiment designed to test the effect of feral cat predation on small mammal populations.

85 It has been suggested that predation by feral cats is not the main cause of recent mammal declines
86 in northern Australia. The main argument used for this suggestion is that feral cats have been
87 present in northern Australia for more than a century, but declines in some native small mammals
88 are relatively recent (Abbott, 2002; Short and Calaby, 2014). There are no data on changes in feral
89 cat abundance in recent decades that might explain the more recent declines. A range of other
90 factors, such as changed fire regimes, grazing by introduced herbivores, disease and trophic
91 cascades resulting from cane toad (*Rhinella marina*) invasion have also been proposed as
92 contributing factors to declines in small mammals (Ziembicki *et al.*, 2015), or (for fire and introduced

93 herbivores) as factors that compound the effects of predation by feral cats (e.g., with consequent
94 habitat change resulting in increased abundance and/or hunting success of cats (McGregor *et al.*,
95 2014; Legge *et al.*, 2019; Davies *et al.*, 2020). Effective management, to maintain or restore native
96 mammal populations in northern Australia needs more evidence about the relative effects of the
97 different threats, and their interactions, in different landscape and management contexts.

98 Compelling evidence implicating predation by feral cats as a cause of small-mammal decline in
99 northern Australia comes from the experimental study of Frank *et al.* (2014). In that study, native
100 long-haired rats (*Rattus villosissimus*) were released into two replicates of experimental enclosures,
101 in which each replicate provided one area accessible to cats and one (otherwise comparable) area
102 prevented access to cats. Populations of long-haired rats in both enclosures exposed to cats were
103 extirpated, declining rapidly in the enclosure where cat incursions were frequent, and declining
104 slowly in the other enclosure where incursions were less frequent. In contrast, the populations of
105 long-haired rats in the two enclosures that were not exposed to cats persisted over the study period
106 (18 months) and maintained some recruitment.

107 Although the Frank *et al.* (2014) study demonstrated that cats can drive declines of local populations
108 of native mammal species, some considerations limited the generality of the results to other
109 northern Australian mammal species. First, the model species may be unrepresentative of the north
110 Australian mammal fauna, given that the long-haired rat has not exhibited a severe and pervasive
111 decline in northern Australia (Woinarski *et al.*, 2011) – although, subsequent evidence has suggested
112 an ongoing decline across much of its range (Bonyhardy, 2019). Secondly, unlike some other
113 mammal species in Australia’s monsoonal tropics, it has a boom-bust life cycle and consequently
114 may have an atypical individual and population-level response to predation (Greenville *et al.*, 2013).
115 Thirdly, the individual long-haired rats used in the Frank *et al.* (2014) study were obtained from a
116 single cat-free island and most were subsequently kept between capture and release in captivity
117 (6.5% of those released), or were first generation captive-bred descendants from this population

118 (93.5%). Therefore, the animals used in Frank et al. study may have had some level of predator-
119 naivety (Sih *et al.*, 2010; Moseby *et al.*, 2018).

120 In this study, we repeat Frank et al.'s (2014) study, with two modifications. First, we used the native
121 pale field rat (*Rattus tunneyi*) as the study species because it is recognised to be undergoing broad-
122 scale population declines throughout the tropical savannas of northern Australia, and is listed as
123 Vulnerable in the Northern Territory (Braithwaite and Griffiths, 1996; Woinarski *et al.*, 2011). This
124 species may, therefore, be more representative and provide more insight into the pattern and
125 causality of decline for north Australian mammal species more generally. Second, all rats were
126 sourced from a population where feral cats are present and known to prey on *R. tunneyi* (McGregor
127 *et al.*, 2015a; Leahy *et al.*, 2016), and were released into the experimental enclosures in a wild-to-
128 wild translocation without staging them in captivity. Using animals with prior exposure to feral cats
129 better reflects mammal populations on mainland northern Australia and avoids the potentially
130 confounding effects of predator-naivety (Jolly *et al.*, 2020).

131 Based on the hypothesis that feral cats are key drivers of population decline in northern mammals,
132 we predicted that pale field rats, in cat-inaccessible enclosures, would show greater survivorship
133 than those in cat-accessible enclosures. In addition, if pale field rats sourced from the wild are less
134 prone to cat predation than the predator-naïve long-haired rats used in the previous study, we
135 predicted their survivorship in the cat-accessible enclosures should be greater than the translocated
136 long-haired rats used in the previous trial.

137 **Materials and methods**

138 *Study area*

139 As with the Frank et al. (2014) study, the experiment was conducted at Wongalara Wildlife
140 Sanctuary, a reserve owned and managed by the Australian Wildlife Conservancy (Figure 1). The
141 habitat is open tropical woodland with a ground layer of low shrubs with sparse grass. The climate is

142 monsoonal, with mean annual rainfall of 1,050 mm, falling predominantly between December and
143 April (Australian Bureau of Meteorology). Temperatures range from mean minimum 14°C in July to
144 mean maximum 39°C in November. The Australian Wildlife Conservancy has managed the Sanctuary
145 for conservation purposes since 2006 by preventing large intense wildfires as per Legge et al.
146 (2011b), and by reducing the density of large introduced herbivores (cattle *Bos taurus x indicus*,
147 buffalo *Bubalus bubalis*, horse *Equus caballus*, and donkey *Equus asinus*). The density of feral cats
148 was typical for northern Australia (less than 0.05 per km², AWC unpublished data) and, at the time of
149 the study, there was no ongoing program to control feral cats. The study area is described in more
150 detail in Frank et al. (2014). The site is within the former range of pale field rats (Woinarski *et al.*,
151 2014), but they are now largely absent from the region.

152 *Source population*

153 Pale field rats were sourced from Mornington Wildlife Sanctuary (ca. 950 km distant from the
154 experimental trial) in the central Kimberley in Western Australia, a property also owned and
155 managed by the Australian Wildlife Conservancy (Figure 1). Rats were trapped over one week in
156 January 2014 from four locations within an area from which large introduced herbivores (cattle,
157 buffalo, horses and donkeys) have been excluded (Legge *et al.*, 2011a). Rats were trapped using
158 Elliott traps baited with oats and peanut butter. The source habitat consisted of open tropical
159 woodland on sandy soils with a dense grass layer. This habitat was broadly similar to the area that
160 rats were translocated into, with the exception that ground cover at the release site varied in
161 composition, with some areas dominated by heath and others by grasses, including spinifex. Feral
162 cats were present at the source site, at densities of 0.1 – 0.26 per km² (McGregor *et al.*, 2015b).

163 *Experimental design*

164 We translocated pale field rats into two sets of paired enclosures (13 km apart; Figure 2) in the same
165 experimental design used by Frank et al. (2014). Both enclosures were located on the same

166 sandstone plateau. The habitat in the enclosures at Site 1 was sparse shrubs and grasses with high
167 density tree cover. In the enclosures at Site 2, shrubs and grasses were more dense and there was a
168 lower density of trees. Each site consisted of paired enclosures of 6.25 ha each, one with a low fence
169 (0.9 m) that cats could leap over but rats could not escape through, and one with a high fence fitted
170 with a floppy top and electric hotwires designed to exclude cats (Moseby and Read, 2006). All
171 experimental enclosures had a lower 0.6 m panel of thick plastic dug into the ground to prevent rats
172 escaping by burrowing under the fence or climbing through it.

173 *Translocations*

174 We selected 42 adult rats for translocation. Adults were defined as weighing more than 60 g
175 (Braithwaite and Griffiths, 1996). Rats were held for between one and five days between capture
176 and translocation until sufficient numbers had been caught. Rats were held in individual purpose-
177 built wooden crates in a cool, dim room, checked twice a day and provided with food and water *ad*
178 *lib*. Thirty-six rats of the 42 (those weighing over 80 g) were fitted with radio-collars weighing 2.6 –
179 3.2 g (Sirtrack Lite VHF transmitters). All rats were microchipped for individual identification.

180 All rats were transferred from Mornington to Wongalara on 8 January 2014 by light plane on a five-
181 hour journey. They were sorted to maintain comparable sex ratios and then randomly assigned into
182 four groups and released into the enclosures on dusk, with nine radio-collared rats released per
183 enclosure. Ten rats (6 males, 4 females; 9 with radio-collars) were released into each enclosure at
184 Site 1, and 11 rats (7 males and 4 females; 9 with radio-collars and two without) into each enclosure
185 at Site 2. The sex ratio of rats released into enclosures at Site 1 and Site 2 was 0.6 and 0.64 M:F
186 respectively. No rats were naturally present in any enclosures at the time of these releases.

187 *Monitoring*

188 Rat survival was monitored by locating all radio-collared individuals at least once every three days
189 for three months after release. Rats that died were located as soon after death as possible to

190 determine cause of mortality. Rats were captured using 50 Elliott traps over three nights at each
191 enclosure at two months, four months and ten months after release to assess body condition and
192 breeding status, to monitor rats not fitted with radio-collars, and to monitor recruitment of young
193 born on-site. Body condition was assessed by scoring the amount of fat between the spine and hips.
194 Cat visitation to enclosures was monitored using arrays of 24 infrared camera traps (Reconyx
195 Hyperfire Professional) at each site that were checked every week. Cameras were unbaited and
196 placed inside each of the four enclosures and around the perimeters at approximately 100 m
197 intervals. Cameras were deployed in this way for three months prior to the translocation, and in
198 fewer numbers but continuously over the 18 months before the three-month lead-up to the
199 translocation. Cats continued to be monitored on these camera traps for two months after the
200 translocations, with the addition of opportunistic searches for tracks in the sand and nighttime
201 spotlighting around the perimeter of each enclosure. The timing of each cat visit was noted and,
202 where possible, individual cats were identified from unique pelage markings.

203 *Statistical analysis*

204 We used Cox-proportional hazard modeling (Hosmer and Lemeshow, 2008) to investigate the effect
205 of enclosure, cat accessibility (fence), rat sex and cat visitation on survival of the translocated pale
206 field rats. Analyses were performed using the “survival” package in R version 3.1.2 (Therneau, 2015).
207 Rats were classed as either alive or dead at the end of the study, with individuals that left the study
208 (‘missing’ or ‘fate unknown’) right-censored at the last point the animal was reliably recorded as
209 alive. The effect of the fencing treatment on mortality was measured at time t for each individual,
210 where t = number of days since release. The hazard model used was:

$$211 h(t) = h_0(t) \exp(\beta_1 \text{Cat}(t) \cdot \text{Site} \cdot \text{Fence} \cdot \text{Rat Sex})$$

212 Where the hazard $h(t)$ was the mortality risk, $h_0(t)$ was the baseline hazard and $\text{Cat}(t)$ was a time-
213 dependent covariate describing cat exposure with two levels, ‘yes’ and ‘no’ as cat detections varied

214 over time and with accessibility (high versus low fence). Since cats were only ever detected within
215 our designated cat-accessible low fences (as intended in the experimental design), cat exposure was
216 always classed as 'no' for cat-inaccessible high fence enclosures. Once a cat was first detected in an
217 enclosure, all subsequent days were classed as 'yes' for cat exposure. The remaining covariates were
218 not time-dependent: site (1 or 2), fence (high or low) and rat sex (M or F).

219 The assumption of proportional hazards for the covariates and the model was tested by correlating
220 the corresponding set of scaled Schoenfeld residuals against time (Hosmer and Lemeshow, 2008).

221 **Results**

222 *Rat survival*

223 Seventeen of the 18 radio-collared rats introduced into Site 1 died within the first three months of
224 the translocation, nine of them in the cat-accessible (low fence) enclosure and eight in the cat-
225 inaccessible (high fence) enclosure (Figure 3). Twelve of the 18 radio-collared rats introduced into
226 Site 2 died within the first three months of the translocation, all nine of those in the cat-accessible
227 and three of the nine in the cat-inaccessible enclosure (Figure 3). Rats that were exposed to cats
228 (within low fence enclosures, after a cat had been detected) were 6.2 times (95% CI: 4.7 – 8.1) more
229 likely to die as compared to those not exposed to cats ($z = 13.2$, $p < 0.0001$; Table 1). Individuals in
230 cat-inaccessible treatments had a 59% lower risk of death than those in cat-accessible treatments
231 regardless of cat visitation (hazard ratio of 0.41, 95% CI: 0.3 – 0.5; $z = 6.6$, $p < 0.0001$; Table 1).
232 Survival rate was 1.3 times greater in Site 2 (95% CI: 1.2 – 1.4) compared to Site 1 ($z = 6.4$, $p <$
233 0.0001). Male rats had a 25% lower risk of death than female rats (hazard ratio of 0.75, 95% CI: 0.7 –
234 0.8, $z = 7.3$, $p < 0.0001$; Table 1).

235 At three months after release, one of nine radio-collared rats remained alive in the cat-inaccessible
236 enclosure of Site 1; and no radio-collared rats remained alive in the cat-accessible enclosure of Site

237 1. Six of nine radio-collared rats remained alive in the cat-inaccessible enclosure at Site 2; no radio-
238 collared rats remained alive in the cat-accessible enclosure of Site 2.

239

240 *Cat visitation*

241 Two individual cats, one at each site, were recorded visiting the cat-accessible enclosures after rats
242 were released. On every occasion, the cats were recorded on several cameras within the enclosures
243 over a period of hours. A cat was first observed visiting Site 1 at 30 days post-release. This same cat
244 returned to the enclosure later the same week and again every week thereafter. The cat was
245 identified from camera trap images as a tabby that had visited the enclosure in October 2012 and
246 again in October 2013, 15 and three months prior to the translocation respectively. Site 2 was first
247 visited by a cat on the first night after rats were released in January 2014. This cat was black and
248 therefore a different individual to the cat recorded at Site 1. It was possibly the same individual that
249 had preyed on long-haired rats in the 2012 translocation (reported in Frank et al. 2014). If so, this
250 was the first observation of that individual cat since August 2013, five months before the
251 translocation, despite continuous deployment of camera traps in the intervening period. The same
252 cat visited two nights later and again over the following four nights. It was recorded again at 29 days
253 post-release and regularly visited between 50- and 80-days post-release. No cats were detected in
254 the cat-inaccessible treatments; nor were any of the enclosures ever visited by the other large-
255 mammalian predator in the area, the dingo *Canis lupus dingo*.

256

257 *Cause of mortality*

258 Cat predation was inferred as the cause of death for eight rats in the cat-accessible enclosure at Site
259 1, and for nine rats in the cat-accessible enclosure at Site 2 (Table 2). Eleven rats were found with
260 signs of cat predation, including broken necks and puncture marks that matched cat canines. For the
261 three rats in cat-accessible enclosures where cause of death could not be easily deduced from the
262 remains, the timing of cat visits corresponded with the dates of death of these rats. The three rat

263 deaths in the cat-accessible enclosure at Site 1 that occurred prior to the first cat detection were all
264 within two days of the cat being detected and showed signs of cat tooth marks on the remains and
265 radio-collars. All but one of the nine mortalities in the cat-accessible enclosure at Site 2 took place
266 during the eight days of visits by cats that occurred immediately after release of the rats. The last rat
267 died during another spate of cat visits two months after the release. One rat in the cat-accessible
268 enclosure at Site 1 died of misadventure, being caught by the radio-collar in a pile of woody debris.
269 The black cat that visited Site 2 was detected on a camera trap outside the enclosure with a rat in its
270 jaws eight days after the release. The extremely low density of *in situ* small mammals in the study
271 area outside the experimental enclosures (average of 0.3 animals per trap night at the time of the
272 study, AWC unpublished data), with no records of native rats, makes it highly likely that the rat
273 pictured was a translocated animal.

274 One of the eight rats that died in the cat-inaccessible enclosure at Site 1 died within 12 hours of
275 release, from unknown causes, and no signs of predation were visible when it was found. Six were
276 killed by pythons and goannas (as evidenced by radio-collars being found within a python or in a
277 goanna scat) and one's fate was unknown. Two of the three rats that died in the cat-inaccessible
278 enclosure at site 2 were most likely killed by aerial predators such as owls (remains were located far
279 from the enclosures and beneath perches) as mammalian predators were never recorded within the
280 high-fence treatment. Another was killed by a python (the radio-collar was found within the snake).

281 None of the six individually marked rats released without radio-collars were re-trapped in any
282 trapping session. The surviving rats that were trapped at two months and four months after release
283 maintained body condition. Recruitment was observed only at the cat-inaccessible enclosure at Site
284 2, where six new individuals (four female and two male) were captured between six and nine
285 months after release. When rats were trapped at ten months after release, they were all in good
286 condition and some were recruits (of the five animals caught, four were new recruits).

287

288 **Discussion**

289 This study demonstrates the ability of cats to extirpate local populations of a small mammal species
290 in the tropical savanna of northern Australia. Populations of pale field rats exposed to cats were
291 rapidly extirpated, even though those animals were translocated from sites with cats and into an
292 area with a low density of cats and good vegetation condition. Rat populations translocated into
293 enclosures that were accessible to cats declined rapidly to extirpation after cats first entered the
294 enclosures, with no rats surviving for longer than 80 days after release. In contrast, rats not exposed
295 to cats persisted for at least three months after release at one site and at least nine months after
296 release at the other. Seventeen of 18 rat deaths within cat-accessible enclosures were attributed to
297 cat predation, while seven out of 11 rat deaths within cat-inaccessible enclosures were attributed to
298 native predators (raptors, goannas, pythons). Rats exposed to cats were six times more likely to be
299 killed than rats that were not exposed to cats. Female rats had lower survival than males, suggesting
300 that the smaller bodied females may have been more vulnerable to predation by cats that may
301 prefer smaller prey (Childs, 1986) or compromised in some way by greater metabolic requirements
302 of pregnancy or lactation.

303 Pale field rats exposed to cats had much lower survival than rats in cat-free enclosures, providing
304 further experimental evidence that feral cats play a role in mammal declines in northern Australia
305 (Frank *et al.*, 2014; Ziembicki *et al.*, 2015). Our prediction that pale field rats in cat-accessible
306 enclosures should have better survival compared with long-haired rats in the previous translocation
307 (Frank *et al.* 2014) was not supported. We expected better survival rates among pale field rats for
308 two reasons. First, pale field rats do not have a strong boom-bust demographic cycle and are more
309 likely to exhibit predator-wary behaviours. While predator avoidance behaviours were not assessed,
310 long-haired rats in the Frank *et al.* (2014) study were observed noisily moving through the leaf litter
311 at times, while pale field rats were more cryptic in their movements (K. Tuft, personal observation).
312 Second, pale field rats were sourced from a population that had prior exposure to cats, unlike the

313 long-haired rats that were sourced from a cat-free island and were mainly bred in captivity (Frank et
314 al. 2014). However, such was the predation pressure exerted by the cats, that even with prior
315 exposure to cats, survival rates of pale field rats were no better than those for long-haired rats.

316 At each site, it appears that a single cat was responsible for all cat predation mortalities of rats.
317 Moreover, the cat detected at Site 2 was the same individual responsible for the extirpation of long-
318 haired rats at this site 21 months earlier. If so, it suggests that cats may revisit potentially profitable
319 hunting grounds. A similar phenomenon has been observed with feral cats revisiting areas burnt by
320 intense fires for several months after the fire (McGregor *et al.*, 2016). Return visits by cats to sites at
321 which they have previously located prey species may be a feature that renders communally denning
322 native mammal species particularly susceptible, as individual cats can successively take all individuals
323 from a colony. Individual cats vary greatly in their preferences for prey (Dickman and Newsome,
324 2015); and some can learn to become specialists at hunting a particular prey species (Moseby *et al.*,
325 2015). The rapid depletion of translocated rats could also be due to cats generally showing a
326 preference for hunting mammalian prey (Paltridge *et al.*, 1997; Doherty *et al.*, 2015; Murphy *et al.*,
327 2019), and that small mammals were at low densities on Wongalara at the time of the study (AWC,
328 unpublished data). Cats are adept at hunting scarce and cryptic prey. Dickman and Newsome (2015)
329 found that cats continued to hunt and kill their preferred prey of rabbits (*Oryctolagus cuniculus*)
330 even when the density of rabbits fell so low that they became undetectable in surveys, a result also
331 reported in a study of cat predation on native mammals in the same environment as our trial
332 (Stokeld *et al.*, 2018). Our pale field rat translocation experiment clearly demonstrates that cats can
333 target prey even when they are extremely scarce in the landscape.

334 If cats prefer to hunt mammalian prey, even at very low density, small mammals may fall into a
335 predator sink where recruitment and dispersal cannot outpace predation by cats and other
336 predators, leading ultimately to population extirpation (Pech et al., 1995). The effect of cats
337 observed in this study was potentially exacerbated by translocation of pale field rats into a small

338 enclosed area at relatively high density surrounded by habitat where small mammals are at
339 extremely low densities. Cats are likely able to optimise their predation rate by focussing on sources
340 of prey that yield better returns.

341 It is alarming that cats were able to extirpate the rats so rapidly, despite the very low densities of
342 feral cats on Wongalara at the time of the study (less than 0.05 per km², AWC unpublished data from
343 camera trap estimates). This density is lower than the source population from which the pale field
344 rats were taken (0.1 – 0.26 per km², McGregor *et al.*, 2015b) and lower than the national average of
345 0.27 per km² (Legge *et al.*, 2017). Nonetheless, those cats present at the site were able to detect the
346 translocated rats and hunt them to local extinction within two months. The severity of cat predation
347 compounds that of native predators. Goannas, snakes and raptors caused 53% of the mortalities in
348 the cat-inaccessible areas, suggesting that predation pressure in general was high at Wongalara.
349 Some attrition to native predators must be factored into planning translocations.

350 Rat mortality was overwhelmingly caused by predation (95%), and there was little evidence that
351 habitat quality or resources alone were limiting factors over the timescale of the study. The study
352 occurred during the wet season, when food resources for pale field rats and protective ground cover
353 were at their seasonal peak. After the translocation, the animals did not show any loss of condition
354 to indicate resource stress. The area of each enclosure (6.25 ha) should have been adequate to
355 support sufficient home ranges for the number of rats translocated (home ranges estimated at 0.09
356 ha for females and 0.39 ha for males at the source site; Leahy *et al.*, 2016).

357 Habitat complexity may have affected predation risk of translocated pale field rats to cats and native
358 predators (Lawes *et al.*, 2015). While ground cover density at Site 2 was approximately equivalent to
359 that at the source site, ground cover was sparser at Site 1 (Frank *et al.*, 2014). Within the cat-
360 accessible enclosures, ground cover at 10 cm height at Site 2 was twice that of Site 1 (16.7% and
361 34.8% respectively; I. Radford unpublished data). The sparser vegetation at Site 1 may have
362 increased rats' visibility to predators and provided fewer refuges to flee to, potentially explaining the

363 difference in survival observed between sites. Rat survival was better, recruitment occurred, and
364 rats were still present ten months after translocation in the cat-inaccessible enclosure at Site 2
365 where there was a denser ground cover of vegetation. A similar trend of a slower decline at the site
366 with denser ground cover was observed for long-haired rats exposed to cats in Frank *et al.* (2014).

367 What then can we do to reverse the current small mammal declines in northern Australia? There is
368 evidence that the effects of cat predation can be mitigated, to some extent, by managing habitat to
369 provide refugia (or denser ground cover) to prey animals (Ziembicki *et al.*, 2015). Management of
370 fire to retain unburnt habitat improves habitat quality (Legge *et al.*, 2011b) that in turn reduces the
371 hunting efficiency of cats (McGregor *et al.*, 2014; McGregor *et al.*, 2015a), and results in greater
372 survival of small mammal prey (Leahy *et al.*, 2016). Similarly, retention of, or increase in, ground
373 cover through removal of large introduced herbivores (cattle, horses and donkeys) leads to
374 population increases in small mammals (Legge *et al.*, 2011a). In this study, the greater survival for
375 rats at the site with denser ground cover corroborates that habitat complexity close to ground level
376 is important for small mammals, potentially by moderating predation impacts. At the time of this
377 study, eight years of active fire management by the Australian Wildlife Conservancy had resulted in
378 fewer intense fires and greater proportional extent of long-unburnt vegetation across Wongalara
379 (AWC, unpublished data). In addition, feral herbivores were removed from much of the property two
380 years prior to the translocation experiment. Despite these efforts, *in situ* populations of small
381 mammals had not recovered on the property at the time of the study (AWC, unpublished data), and
382 our study suggests that standard translocations alone are likely to be insufficient to re-establish
383 populations of small mammals when general levels of small mammals are low, despite there being
384 food and shelter available. Future translocations may need to be accompanied by targeted and
385 sustained control of feral cats. In our study, two individual feral cats were able to extirpate all the
386 accessible rats, reinforcing the need to effectively control cats, over an enduring period, prior to and
387 during future translocations (Moseby *et al.*, 2015; Read *et al.*, 2016) to mitigate predation sinks.
388 Substantially increasing the numbers of animals translocated may also be necessary to improve the

389 chance of successful establishment by ‘swamping’ the remaining cats, although such an approach is
390 dependent on large source populations to translocate from and may still be unsuccessful (Bannister
391 *et al.*, 2016). It is increasingly clear that feral cats are a major driver of declines of mammals in
392 northern Australia, and it appears that in places like our study site, if native mammals persist at all,
393 they do so in small populations subject to predator sink effects from which recovery is
394 compromised.

395 This research is further evidence of the effectiveness of invasive predators, even at very low
396 densities, to extirpate populations of native prey. Predator sink effects where native prey
397 populations are sparse can compromise recovery of these species in invaded landscapes even where
398 other threats such as fire and grazing are managed. More intensive conservation actions may be
399 necessary to elicit recovery in these cases.

400

401 **Author’s contributions**

402 KT, SL, JW and CJ conceived the ideas and designed the methodology with contributions from IR, AF,
403 ML and IG. KT, SL, TM and EP collected the data. KT analysed the data and led the writing of the
404 manuscript. All authors contributed critically to the manuscript. The authors declare no conflicts of
405 interest.

406

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416

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539 implementing management responses for the disappearing mammal fauna of northern Australia.
540 *Therya* **6**, 169-225

541

542 Table 1. Cox-proportional hazards coefficients, standard errors, Wald statistics (z) and
 543 probability values for risk of mortality for radio-collared pale field rats modelled as a function of cat
 544 exposure, site, fence and sex.

545

Parameter	β	SE	z	p	hazard ratio	95% CI
Cat (yes)	1.82	0.14	13.24	< 0.0001	6.21	4.73 – 8.14
Site (1)	0.26	0.04	6.44	< 0.0001	1.30	1.20 – 1.41
Fence (cat-inaccessible)	-0.90	0.14	-6.57	< 0.0001	0.41	0.31 – 0.53
Sex (M)	-0.29	0.04	-7.31	< 0.0001	0.75	0.69 – 0.81

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550 Table 2. Fate of radio-collared rats translocated into each enclosure.

Cause of mortality	Site 1		Site 2	
	Cat-accessible	Cat-inaccessible	Cat-accessible	Cat-inaccessible
Total released	9	9	9	9
Cat predation	8		9	
Bird of prey predation				2
Reptile predation		6		1
Misadventure	1	1		
Unknown		1		
Alive after 80 days	0	1	0	6

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556 **List of figures**

557 Figure 1. Map of study location including source site (Mornington) and translocation site

558 (Wongalara).

559 Figure 2. Schematic diagram of the experimental setup. Both enclosure-pairs were constructed

560 identically.

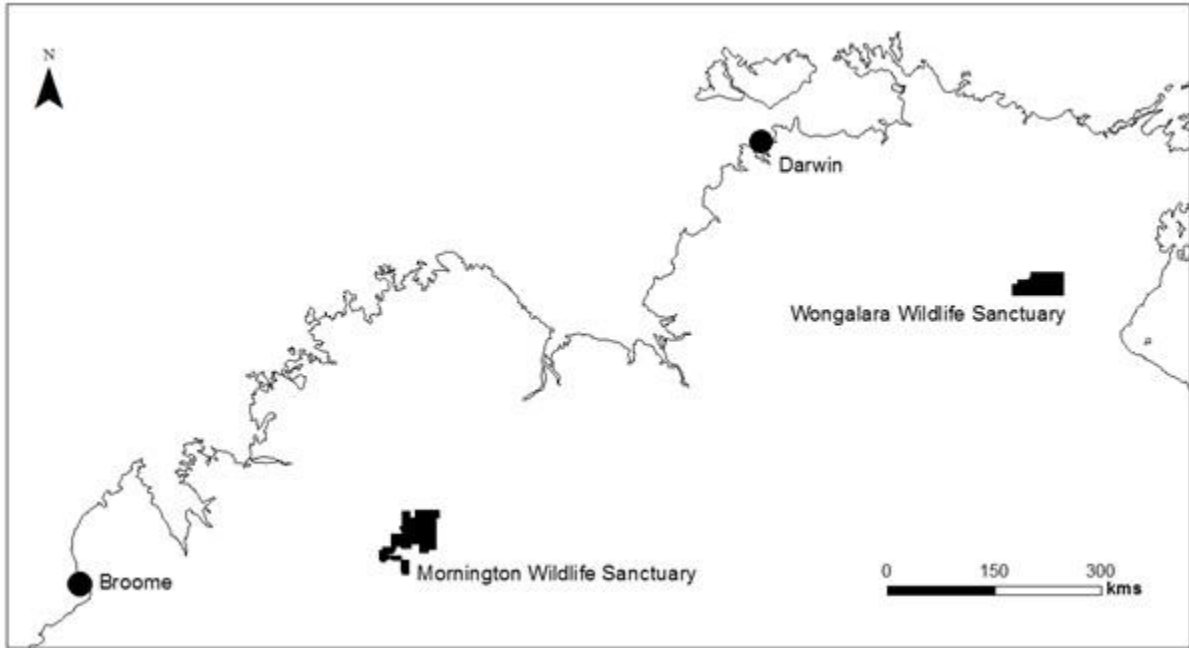
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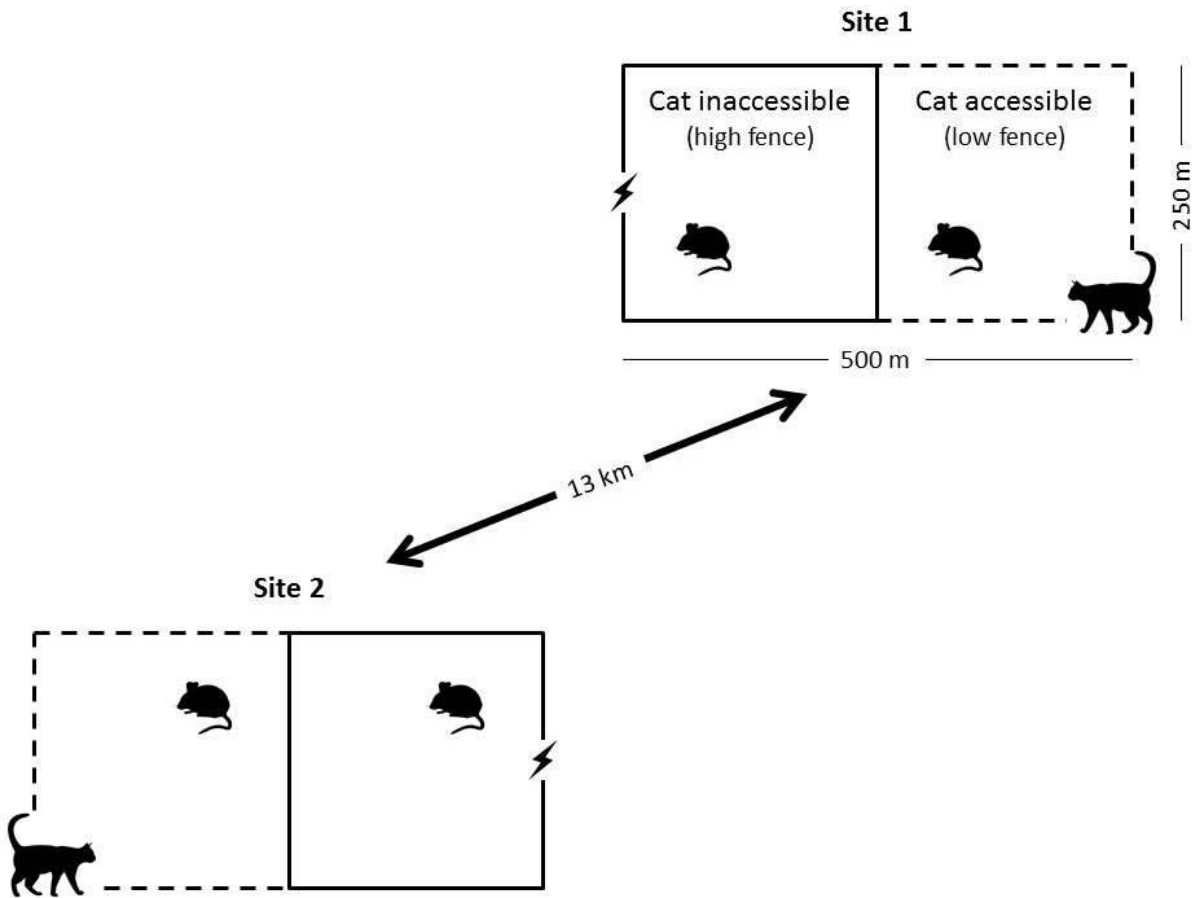
562 Figure 3. Number of radio-collared *R. tunneyi* individuals alive plotted against time since release at

563 sites 1 and 2. Cat detections are indicated with grey bars and rat deaths identified as cat predation

564 are indicated with an asterisk.

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