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The short-term response of feral cats to rabbit population decline: are alternative native prey more at risk?

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19 Author contributions

- 20 All authors conceived the ideas and designed methodology; HM collected and analyzed the
- 21 *data; HM led writing of the manuscript; and all authors contributed critically to the drafts*
- 22 *and gave final approval.*

23 Compliance with Ethical Standards

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38 Abstract

The impacts of invasive predators can be amplified by high densities of invasive prey species. This is evidently the case in Australia, where hyperabundant rabbit populations lead to high densities of feral cats and correspondingly high impact of cats on native species, especially small mammals. This suggests that reducing rabbits could also reduce abundance of cats, and thereby alleviate predation on native small mammals. However, cats might respond to the loss of rabbits by prey-switching to native small mammals, resulting in increased predation on those species.

46 We investigated the short-term effects of an experimental reduction of rabbit abundance on

47 feral cats and their small-mammal prey in arid South Australia. We reduced the rabbit

48 population in a 37 km² experimental enclosure by ~ 80% (2,215 rabbits removed from an

49 estimated population of ~2,800), while monitoring an adjacent unmanipulated area as a

50 control. Cats were present in both the experimental and control areas.

Cat activity and survival of VHF-collared cats in the enclosure decreased by 40% following the rabbit reduction. Surviving cats increased their consumption of reptiles, birds and invertebrates, but they nevertheless evinced hunger by increased their intake of experimentally-supplied sausages, and by losing body condition. There was no change in either the proportion of cat scats that contained remains of small mammals, or the rate at which video-collared cats were recorded killing small mammals, even though the activity of small mammals declined.

58 Our results demonstrate that individual feral cats prey-switch in response to removal of their 59 primary prey. However, we also show that survival and overall activity of cats decreased, 60 which could result in net, long-term benefits for native prey threatened by cats. Management 61 of feral cats using food lures or baits would also be more effective when introduced prey are 62 scarce, as cats are more likely to eat novel food.

63 Introduction

64 Invasive predators are a major threat to biodiversity worldwide, often having greater impacts

on prey than do native predators (Paolucci et al. 2013). This can be due to several factors,

66 including lack of co-evolution between introduced predators and native prey resulting in prey

naïveté (Griffin et al., 2000; Moseby et al. 2016), specific morphological and behavioural 67 traits that give some invasive predators an advantage (Vermeij 1991, Webb 1985), or 68 anthropogenic disturbances that shift habitats or communities to states that favour invasive 69 predators. The latter factor may be especially relevant to the biological invasions 70 accompanying European colonisation across the world over the last 400 years, which has 71 72 often involved the introduction of novel prey species as well as predators. These novel prey may elevate the densities of invasive predators and lead to hyper-predation on native prey 73 74 (Abrams et al. 1998, Courchamp et al. 2000).

75

76 In Australia, invasive feral cats Felis catus and red foxes Vulpes vulpes threaten many species of native wildlife, especially native mammals between 35g and 5,500g in body mass 77 78 (Burbidge and Manly 2002, Woinarski et al. 2015). The regions with the greatest loss of mammals have been the arid and semi-arid zones of southern Australia (Smith and Quin 79 80 1996), coinciding with the regions where densities of the invasive European rabbit 81 Oryctolagus cuniculus have historically been highest. This suggests that at least part of the 82 explanation for the large impact of invasive predators on native prey in these regions could be the effect of rabbits in sustaining high population densities of feral cats and foxes. Therefore, 83 84 managing populations of invasive herbivores that are important prey of cats and foxes, such as rabbits, may provide a tool for indirect control of invasive predator populations (Pech et al. 85 1992, Pedler et al. 2016). Such control could be in the form of direct suppression (for 86 example, by ripping rabbit warrens or poison-baiting) or the introduction of bio-control 87 88 agents such as Rabbit Haemorrhagic Disease Virus (RHDV).

89 Reducing the population density of an invasive predator by manipulating populations of 90 invasive prey could reduce the intensity of predation on alternative native prey (Courchamp et al. 2000). It is also possible that as invasive prey decline the predators switch to native 91 92 prey, and thus increase predation rates on those native species, at least temporarily (Murphy et al. 2005). When RHDV was released as a biocontrol agent to the Australian rabbit 93 population in 1995/96, the resulting epidemic caused widespread decline of rabbits, and 94 associated declines in populations of feral cats and red foxes. During this period, studies 95 96 investigating the diets of cats and foxes through scat and stomach contents found that the 97 proportion of native animals in their diets increased (Holden and Mutze 2002, Moseby et al. 1998, Pech and Hood 1998, Read and Bowen 2001). The impact of such prey-switching on 98 populations of native prey is disputed (Doherty et al. 2015a, Mutze 2017), mainly because it 99

is not clear whether the magnitude of prey-switching during the period of predator decline is
large or sustained enough to drive populations of native prey to local extinction, and whether
the eventual benefit of lowered density of invasive predators outweighs the transient impact
of prey switching.

104 Our understanding of the impacts on native prey of prey-switching by feral cats and foxes is 105 limited by the fact that to date all evidence of the phenomenon comes from analysis of diet 106 composition from scats or stomachs of predators. These analyses do not necessarily reveal changes in the rate of predation on prey populations, for three reasons. First, consumption of 107 108 native prey is measured as frequency in the diet, rather than as an absolute kill rate per unit time. A decline in consumption of invasive prey could increase the frequency of native prey 109 110 even if the absolute kill-rate of native prey does not change. Second, when cats and foxes are sated, they may still kill surplus prey without consuming them (Kruuk 1972, McGregor et al. 111 2015, Short et al. 2002). This makes it possible that kill rates per predator may decline 112 following a decline in primary prey, but that intake rates remain the same because predators 113 are eating more of the native animals they have killed. Third, differentiating between freshly-114 killed prey and carrion is unreliable from scat and stomach analysis. A more detailed 115 understanding of how cats respond when their primary prey populations are reduced is 116 essential to assess the effects on native prey of prey-switching. 117

The total impacts of prey-switching also depend on the density of predators. A reduction in available food could lead to a reduction in predator numbers, potentially offsetting any impacts of individual-based prey-switching. But understanding the effect of this on populations of native prey depends on knowledge of the factors that affect survival of cats following reduction of food, including whether they move to seek prey elsewhere.

To gain a better understanding of the mechanisms underpinning prey switching by feral cats 123 and their potential impacts on native wildlife, we conducted a Before/After/Control/Impact 124 study of feral cats and their prey during a population reduction of rabbits in central Australia. 125 126 The study was conducted at the Arid Recovery Reserve in northern South Australia, which includes a landscape-scale (37 km²) enclosure occupied by feral cats, rabbits and native small 127 128 mammals. The rabbit population in the enclosure was experimentally reduced by ~80% in a 129 30-day period, simulating the magnitude and speed of population decline that would be 130 produced by arrival of RHDV. A neighboring unfenced area of similar size and in which no rabbit removal was undertaken was used as a control site. We used this design to answer the 131

- 132 following questions about the effects of abrupt declines in rabbits: (i) do cat activity, body
- 133 condition and survival change? (ii) do cats prey-switch, and do their diets and kill-rates
- 134 change? and (iii) does abundance of alternative prey such as native small mammals decline?

135 Methods

136 *Study area*

This research was conducted in central South Australia, in and around the 123km² Arid 137 Recovery Reserve (30°29'S, 136°53'E). Approximately 60km² of this reserve is surrounded 138 by a feral-proof fence completed in 2001, whilst the remaining 62km² consists of two fenced 139 areas created by 2008 for the purposes of landscape-scale research. The area has an average 140 141 annual rainfall of 170ml (Olympic Dam Aerodrome, BOM), and is mostly characterized by swales containing scattered small shrubs, dissected by longitudinal sand-dunes and some 142 ephemeral creeklines. We worked in the 'Dingo Paddock', a 37-km² fenced area with a 1.6m 143 high feral-proof fence constructed using 40mm gauge wire and a floppy top that curves 144 145 outwards (Moseby et al. 2012). This prevented adult rabbits, dingoes, cats and foxes from entering the paddock, but would not prevent feral cats already resident from exiting. The 146 147 southern boundary of the Dingo Paddock abuts the rest of the Arid Recovery reserve, where 148 there is an abundant population of hopping mice and plains mice. These native mice appeared to be constantly immigrating into the Dingo Paddock across this boundary (Moseby et al. 149 2019). During the study, there was one dingo present in the Dingo Paddock. The surrounding 150 area was used as a control for the study, mostly on the neighboring Stuart Creek Mulgaria 151 Stations (Figure 1). These areas contain similar types and proportions of habitats, but they are 152 also subject to cattle grazing and have greater detection rates of dingoes, kangaroos and emus 153 (Moseby et al. 2018). 154

155 *Study design*

In late February 2017, 2215 rabbits were removed from the Dingo Paddock over a 12-night
period, by shooting from an all terrain vehicle at night as part of Arid Recovery Reserve
management. Carcasses were left on the ground. Rabbit abundance was monitored by
distance sampling, using a vehicle-mounted spotlight along a fixed transect once a month for
three months prior to the reduction effort and for three months afterwards. Surveys followed
a 17.5 km route through the Dingo Paddock and a 18.3 km route through the control area.

Only one side of the vehicle was surveyed. For every animal detected, we recorded its 162 distance from the track as well as the position of the vehicle along transect. Densities of 163 rabbits were estimated using 'Rdistance'. The area was divided into dune and swale zones, 164 densities were estimated separately for the sections of transects passing through these zones. 165 The total population of rabbits was estimated by multiplying the habitat-specific densities by 166 167 the total area of each zone in each of the experimental and control areas. This was then multiplied by 1.3 to account for animals missed that we determined using a thermal camera. 168 This was based on five nights of spotlighting where temperatures were below 20°C, where 169 170 we had an additional person using a thermal camera (FLIR scout III 640, FLIR® Systems, Inc., Wilsonville, USA) who recording how many rabbits were missed by the spotlight user. 171 This person typically recorded 31% more (SE = 4%). 172

173 Track counts

We measured activity of feral cats, rabbits and native small mammals on 77 track transects (Moseby et al. 2018), 39 inside the Dingo Paddock (20 sand dune, 10 creek-lines and 9 swale) and 38 in the control site (20 dune, 8 creek-line and 10 swale). Each transect was 200m long and swept using a steel drag-bar dragged by an all-terrain vehicle late in the afternoon. The next day we counted the number and species of tracks of all mammals that crossed the transect. Track surveys were conducted once before (November 2016) and once after (April 2017) the rabbit reduction.

181 Changes in activity between the two time periods were examined separately for cats, rabbits 182 and native mammals. We ran seven different generalized linear mixed models with various 183 combinations of habitat, session, area and session-by-area interaction terms. These assumed a 184 Poisson error distribution, and individual transect was set as the random term. We compared 185 models using the Akaike Information Criterion for small sample sizes (AICc) and selected 186 the model with the lowest AICc score (Burnham and Anderson 1998).

187 *Cat body condition and survival*

Cats were captured in the Dingo Paddock using cage traps and soft-jaw leg traps (victor #1.5)
with cat urine as lure. Each cat was fitted with a collar containing a VHF beacon (n = 30),
and some were also fitted with either a video collar (discussed in further detail below). Cats
were re-captured at intervals of 3 to 12 weeks by tracking them to their daytime burrow,

placing a cage-trap at the entrance, and digging above the cat's underground location to cause 192 it to run out into the trap. Once captured, cats were placed in a dark bag and processed 193 without sedation. We measured weight and condition (1-5 scale, where 1 denotes close to 194 death and severely malnourished, 5 denotes excellent condition with hip bones and backbone 195 hard to feel through the thick layer of fat). We also collared six cats in the control area. 196 197 However, two were killed as part of ongoing control around reserve and all others left our study region. Given the difficulty of collecting ranging information from cats in the control 198 area, we instead measured the condition of all cats euthanased during normal cat-control 199 200 operations within 20km of the Arid Recovery Reserve over the same time period. We compared the condition of cats inside and outside the Dingo Paddock before and after the 201 reduction effort using a generalized linear model. 202

Survival was analysed for 29 of the 30 cats that were VHF-tracked. The fate of only one cat 203 was unknown, but we believe this cat left the Dingo Paddock as there was still three months 204 205 of battery life predicted from the collar battery, and it was not detected in the subsequent year despite extensive cat-control and remote-camera trapping. To examine the factors 206 influencing cat survival, we used Cox Survival analysis with log-linear distribution and the 207 'survival' library in R (Therneau 2014). Models were evaluated using AIC. Explanatory 208 209 variables considered were pre-versus post-reduction, sex, body weight, and whether individual cats were detected on the southern boundary of the Dingo Paddock where small 210 mammals moved through the fence (Moseby et al. 2019). 211

212 *Prey selection by cats*

We measured changes in cat diet and "assumed hunger" by analyzing scat contents, 213 deploying animal-borne video collars and measuring uptake of supplementary food. For 214 analysis of scat content, we collected scats both inside the Dingo Paddock and in the 215 neighboring control area before and after the rabbit reduction effort. All scats were placed in 216 a paper bag, and the location, date, and likely age of scat recorded. We also collected scat 217 from cats killed in the control area that had full colons. Scat was dried and sent for analysis to 218 Georgeanna Story (Scats About Pty Ltd, Majors Creek NSW), who identified vertebrate 219 220 species, estimated the count of small-mammal individuals and recorded number of 221 invertebrates. We used generalized linear models to examine whether treatment 222 (experimental/control) and time period (pre- and post-reduction) affected the presence of

rabbit in scats, the count of small mammals (all species combined), and the number of allother prey species found in scats (hereafter alternative prey).

225 As scat analysis provides no information on kill rates, and cannot differentiate between carrion and direct kills, we also deployed animal-borne video collars to measure kill rates 226 227 (Loyd et al 2013, McGregor et al 2015). These were deployed throughout the entire study period. Collars were made with modified GoPro Hero 3 White cameras (GoPro Inc, San 228 229 Mateo, California, USA), with extra infra-red LEDs placed next to the lens (920 nm), VHF 230 beacon (Sirtrack, Havelock, New Zealand), additional batteries (Lithium-ion 1300mha), and 231 a delay timer created with Ardunio Atiny85 chips (ATMEL, San Jose, California, USA) that would turn the camera on 11 hours post release. After parts were compiled, they were coated 232 233 in epoxy resin (SC651, Solid Solutions, Bentleigh East, Australia). Working deployments obtained 6-10 hours of footage. All footage was reviewed, and behavior was categorized into 234 one of five classes (still, walking, grooming, investigating a rabbit warren, hunting). 235

236 With data from video-collars on cats, we compared hunting rates of cats before and after the 237 experimental rabbit control. We calculated kill rates per hour for rabbits, small mammals and 'alternative' foods (carrion, insects, small lizards). Each camera deployment was treated as a 238 239 sample unit. We used only deployments that were active for more than 50 minutes to estimate kill rates for cats. Rates of hunting on small mammals and alternative prey were compared 240 241 pre- and post- rabbit control using generalized linear models, after log-transformation. We had insufficient sample size of rabbit kills, therefore, we compared visitation rates of cats to 242 243 rabbit warrens as an index of hunting of rabbits by cats before and after the rabbit reduction.

244 Finally, we estimated the hunger of cats by measuring their willingness to eat a novel food source: we placed sausages in front of remote cameras and measured rate of uptake by cats. 245 We used skinless beef Chevaps sausages left in the sun for 6 hours, which increased the 246 smell. Sausages were placed 20 sites in the experimental area and 20 in the control area at 247 three time points: three months before, during, and three weeks after the experimental rabbit 248 reduction. For each cat detected on camera when a sausage was available, we recorded 249 whether it ate or ignored it. Cameras were deployed until we obtained at least 15 instances of 250 251 a cat interacting with a sausage in each of the experimental and control areas. This often 252 involved rebaiting cameras repeatedly until this sample size was reached. The fate of the 253 sausage (eaten, not eaten) was examined using binomial generalized linear models, where the fixed effects were treatment (experimental/control area), time period (pre-/during/ post-rabbit
reduction) and their interaction.

256 **Results**

257 Effectiveness of rabbit reduction

Rabbit reduction was undertaken in the study area for 14 days in February/March 2017, 258 removing 2,215 rabbits. Distance sampling based on spotlighting counts of rabbits estimated 259 a population of 2,756 (95% CI = 2430–3082, or 76/km²) in the paddock before removal, and 260 448 (95% CI = 298–598, or 12/km²) afterwards. No decline in estimated density was detected 261 in the control area $(21/km^2 \text{ before}, 26/km^2 \text{ after}, \text{SE} = 6)$. The distance sampling model was 262 263 best described by a half-normal function (AICc weight of 1) with an effective strip width of 48 m and 33% probability of detection. Rabbit activity from track counts varied among 264 265 habitats, being higher on dunes and lower in swales, and was also affected by the interaction between treatment and period (Fig. 2, delta AICc 28.6 lower than next model, 1516 from null, 266 267 and AICc weight of 1). This model showed a significant drop of rabbit activity of 86% in the treatment area following the experimental rabbit control (-2.1, z= -26.1, P<0.001), but no 268 change in the nearby control area (0.01, z=0.2, P=0.86). 269

270 *Cat activity, body condition and survival*

Cat activity was best explained by a model containing session by paddock (delta AICc 9.6 271 lower than next model, 16.6 from null, and AICc weight of 0.99). In this model, cat activity 272 was initially much higher in the dingo paddock (~5 fold), but the track counts of cats dropped 273 significantly by 32% after the rabbit reduction (95% CI =20-45%, t=-2.29, P=0.024), 274 275 remaining stable in the control area (Figure 2). Condition of captured cats declined in the experimental area following rabbit reduction (Figure 3), but did not change in the control area 276 (t=4.63, P<0.001). During the radio-tracking period before the rabbit reduction two collared 277 cats were found dead, and both had gained weight since original capture and were in good 278 condition. Of 21 cats that were collared at the time of the reduction, nine were found dead 279 within 5 weeks. Each of these cats was in poor condition and had lost weight since initial 280 capture. One radio-collared cat was never detected after the rabbit reduction and probably left 281 the study area. Survival analysis of radio-collared cats estimated a 24-fold decrease in weekly 282 survival probability following rabbit reduction (95% confidence range = 4-156, z = 3.26, 283

P=0.001). This model also included the variable identifying which cats visited the southern boundary of the study area, where abundances of native mice was likely to be greatest because of the proximity to the rest of the fenced reserve (Moseby et al. 2019). Cats living in this region were significantly more likely to survive (model importance = 0.96; model averaged coefficients: est=2.62, z = 2.16, P =0.031, Figure 4), while initial cat weight or sex had little influence on survival (model importance 0.41 and 0.29 respectively, neither model significant).

291 *Native rodent activity*

Activity of native rodents (principally Notomys alexis and Pseudomys australis) on the track 292 transects was best described using a model that included an interaction term of treatment and 293 before/after rabbit reduction (Fig. 2), and habitat (AICc delta 7.6 lower than next model, 1058 294 lower than null, AICc weight = 0.98). In this model, activity was initially higher in the 295 experimental area (23 tracks/200m, se = 4.82, z = 5.56, P < 0.001) than the control area (9.5, 296 297 se = 2.34, z = 5.56, P < 0.001); activity declined in both areas after rabbit reduction (coef = -0.49, se = 0.07, z = -6.67, P<0.001), but substantially more in the experimental area (-2.01, se 298 = 0.13, z=-15.12, P < 0.001). 299

300 *Cat diet and hunting behaviour*

From the 64 cat scats collected, those in the experimental area contained significantly less
rabbit after the rabbit reduction, but significantly more alternative prey such as reptiles,
insects and birds (Table 1). No significant change was detected in frequency of small
mammals (rodents and small dasyurids)_(Table 1).

305 From 27 deployments of video collars on 18 cats, cameras worked on 22, recording a total of 104 hours of footage. However, only 15 of these deployments contained footage where cats 306 were active for over 50 minutes. In total, we recorded 22 hours of cat activity before the 307 308 rabbit reduction and 33 hours after. After the rabbit reduction there were significantly more 309 instances of cats eating carrier (Table 2, coef = -0.5, se = 0.2, t = -2.46, df = 13, $P = 0.028^*$) and small prey items (coef = -1.36, se = 0.48, t = -2.7, df = 13, P = 0.016^*), but no difference 310 in the take of small mammals (coef = 0.07, se = 0.5, t = 0.13, df = 13, P = 0.889). The number 311 of rabbit warrens visited per hour of cat activity was non-significantly greater before the 312 313 rabbit reduction, and this difference was largely driven by footage from one cat who visited

11 warrens in an hour (coef = 0.15, se = 0.58, t = 0.25, df = 13, P = 0.807). Cats were
recorded eating two rabbits before the rabbit reduction. Small mammals eaten were spinifex
hopping mouse (*Notomys alexis*), fat-tailed dunnart (*Sminthopsis crassicaudata*), and either
house mice (*Mus domesticus*) or Bolam's mouse (*Pseudomys bolami*). Reptiles eaten were
small geckos and one *Nephurus* spp (Figure 5). There were three instances of cats
approaching prey but not eating it, two of sleepy lizards (*Tiliqua rugosa*) and one of a
bearded dragon (*Pogona vitticeps*). Carrion was rabbit, and one bearded dragon.

Willingness to consume novel food in the form of sausages increased after the rabbit reduction. From the 120 instances of a feral cat walking past a sausage in the control area (42 before, 45 during and 33 after), no cat ate a sausage. Inside the experimental area, our model including an interaction term of session over paddock indicates cats never ate sausage before the rabbit reduction, but did so after the rabbit reduction (coef = 2.32, se = 0.81, z = 2.89, P = 0.004**).

327 Discussion

The large and abrupt reduction in abundance of rabbits following rabbit control in this study resulted in a decline of feral cat activity and survival. Half the cats in our collared sample died in the two months following the rabbit decline, and those that survived hunted in an area with a replenishing prey source; small mammals entering the experimental area via the fence adjoining the rest of the reserve (Moseby et al. 2019). Yet even those surviving cats lost condition, and showed greater willingness to eat novel food, indicating elevated levels of hunger.

335 Rabbits were the dominant food source for feral cats in this study before the rabbit reduction. Their frequency in cat scats was very high compared with studies conducted post calicivirus 336 337 (Doherty et al. 2015a, Wysong et al. 2019), though similar to those conducted prior (Holden and Mutze 2002, Molsher et al. 1999). The rabbit density in the experimental area (~80km²) 338 was very high by contemporary standards, and although lower than many of the densities 339 reported before RCHC biocontrol of between 100-300km², the high levels of cat activity in 340 341 this area was likely supported by these high rabbit densities. However, at a continental scale 342 rabbits are not necessarily preferred prey of feral cats, and most studies report preferences for small mammals between 35 g and 400 g (Doherty et al. 2015a, Radford et al. 2018). Rabbits 343 are likely to be harder to hunt and kill than are many other prey species due to their size 344

(Jones and Coman 1981, Moseby et al. 2015), and it is possible that many individual cats
within this population became specialized on rabbits (Dickman and Newsome 2015), and
were not as flexible as other individual cats after the reduction in rabbits.

We show that when a large source of rabbit prey was reduced, feral cats prey-switched. They increased their consumption of non-mammalian food. Other studies have also demonstrated this from scat or stomach analysis (Delibes-Mateos et al. 2008, Doherty et al. 2015a, Yip et al. 2015), but we also show using video collars that this also corresponded with an increase in kills per hour.

This prey switching appears to have caused a decline in activity of small mammals (mostly N. 353 alexis and P. australis), suggesting the potential to threaten other native mammals in similar 354 circumstances. However, complicating this interpretation was small mammals also declined 355 in the control area (though not as pronounced), and we did not find evidence of increased 356 hunting from either scat analysis or animal-borne video. One possible explanation is that cats 357 358 did increase their targeting of small mammals, but their incidence in the diet didn't change as 359 small mammals became increasingly rare, as Read and Bowen (2001) and Saunders et al. (2004) found with rabbits. Another explanation could be cats always prefer small mammals 360 361 and there was no change before and after, but the high abundance of cats with the experimental paddock caused a greater rate of attrition of small mammals than outside in the 362 363 control zone. Also, our diet sample sizes were small and only large changes would have been detected. Therefore, although we highlight prey-switching has the potential to threaten native 364 365 mammals, we were not able to demonstrate the underlying mechanistic process.

366 Sudden removal of prey from a potentially destructive predator is both a transient threat to native wildlife and an opportunity for management. Prey switching can greatly increase the 367 likelihood of cats eating novel food sources and carrion, as demonstrated here. This also 368 means cats would be more susceptible to control techniques that rely on hunger, such as 369 poison baiting or trapping with food lures. This has also been shown by Christensen et al. 370 371 (2013) and Algar et al. (2007) who found the impact of poison baiting via a similar novel food source was greatest when the density of cats was high relative to prey availability. We 372 373 suggest conservation managers aiming to reduce cat populations should take advantage of 374 declines in rabbit abundance by targeting baiting programs to such times. Not only could this 375 result in more effective reductions in cat density, but it could also help protect native species during a potential prey-switching period. Alternatively, artificially reducing rabbit abundance 376

prior to control would likely improve the uptake of control methods or help naturally reducecat abundance.

379 The decrease in survival of cats reported here occurred within weeks of reduction of rabbit abundance. The rapidity of this change might have been increased by the extreme heat and 380 381 humidity around the time of the rabbit reduction, potentially giving cats a greater need for 382 energy and moisture. Cats that did not hunt near the boundary of the Arid Recovery Reserve 383 were not sustained on the alternative prey available. Given the potential period for preyswitching is immediate, managers need to be prepared to react quickly to protect vulnerable 384 385 wildlife at such times, and/or take advantage of the increased cat hunger at such times to use cat control options like baiting most effectively. 386

This experimental study supports the descriptive research of the aftermath of the original 387 calicivirus release in 1995-1996, which resulted in an increase in occurrence of alternative 388 prey in diet of feral predators (Molsher et al. 1999, Mutze et al. 1998, Read and Bowen 389 390 2001), but an overall decrease in cat density that would ultimately be beneficial for many 391 species (Pedler et al. 2016). However, it contradicts a recent study by Scroggie et al. (2018) that found no decrease in fox activity despite levels of rabbit reduction similar to our study. 392 393 Our contrasting results might be due to our enclosing perimeter fence, which prevented any cats from the outside getting in, while the study of Scroggie et al. (2018) was conducted in an 394 395 open landscape in which control areas could be quickly reinvaded by dispersing animals. It is possible that the results of this study would not be replicated in an open landscape. Even if 396 397 inherent carrying capacity is locally reduced, predators from outside would continue to come 398 in looking for food. However, if the scale of the rabbit decline and resultant reduction in 399 predator density is very large, such as with calicivirus releases, then even immigration into 400 focal areas could not compensate for local mortality.

When changes to prey availability occur and there are few alternative prey sources, new
equilibriums of predator – prey are soon met (Pech and Hood 1998). The subsequent lower
predator densities may allow secondary prey species that couldn't survive previous cat
densities to again survive. Overall, alternative prey sources for predators should be removed
whenever possible, with this management integrated with further predator control.

Interactions between introduced prey and predators can cause synergistic impacts on native
species (Doherty et al. 2015b). When those predators take relatively fewer native prey per

- 408 capita but predator densities are elevated, then the cumulative predation toll on native species
- 409 would exceed that if predators are at lower density. Even though individual cats consumed
- 410 more rabbits and less native prey before the rabbit reduction, it is unlikely that maintaining a
- 411 large population of feral prey (e.g. rats, rabbits) would mitigate impacts to native species in
- the long term. Reducing major food sources like rabbits, introduced rodents or artificial food
- sources (e.g. town dumps) should be considered as valuable management tools resulting in
- 414 long-term benefits, whilst impacts of prey-switching would be short-term and potentially
- 415 mitigated. If we can manage processes that interact synergistically with feral predators, we
- should have a greater change of reducing the overall impact of invasive predators.

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Figure 1. Map of the study area, showing the Dingo Paddock where experimental removal of
rabbits was conducted, the adjoining fenced reserve, and the area outside the reserve used as
the control. The position of all track transects used to measure activity of cats, rabbits and
small mammals are shown with dots. Inset shows the general location of the study area.



Figure 2. Changes in track counts of rabbits, small mammals and feral cats inside the Dingo
Paddock (rabbit removal area) and Mulgaria (nearby control zone) before and after a major
rabbit reduction effort was conducted in the Dingo Paddock. Grey shading indicates 95%
confidence intervals



Figure 3. Changes in cat condition before and after the rabbit reduction effort within Dingo

536 Paddock experimental, compared to nearby control area.



539

540 Figure 4. Survival of cats in the experimental area following rabbit reduction. 'South fence 541 hunters' were those that were detected on remote cameras on the southern boundary of the 542 study paddock, where availability of small mammals would have been greatest after the 543 rabbit reduction effort. This southern boundary abuts the rest of the reserve, where there are 544 high densities of native rodents; these rodents easily pass through the fence.



Figure 5. Images from video-collars deployed on cats, of a cat investigating but not eating a
bearded dragon (a), eating a *Nephurus* spp. (b), consuming the intestines of a rabbit (c), and

550 catching a spinifex hopping mouse (d).

Table1. Count of prey in scats collected from cats before and after the rabbit reduction in the

553 Dingo Paddock, and a nearby control area where rabbit populations remained stable over the

same time period.

	Dingo Paddock		Outside			
	before	after	 before	after	t	Р
Scats (n)	26	12	14	12		
rabbits	0.81	0.42	0.57	0.25	-2.21	0.031*
alternative prey ¹	0.81	2.67	0.79	1.42	4.33	0.001***
small mammals ²	0.88	0.58	0.57	1.17	-0.4	0.688

555

1 Includes birds, reptiles and insects. 2 Includes rodents and small dasyurids

Table 2. Hunting and food consumption events by feral cats witnessed on animal-borne

557 video-collars before and after a major rabbit reduction effort.

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559

	Events	witnessed	Events per ho	Events per hour of activity		
	Before	After	Before	After		
Rabbits	2	0	0.12	0		
Small mammals	5	3	0.19	0.2		
Alternative prey ¹	2	30	0.11	0.37		
Carrion	0	5	0	0.13		
Investigate rabbit warren	37	22	3.56	0.98		

560 ¹ Includes reptiles, insects and small unidentified items consumed.