



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

Hugh McGregor · Katherine Moseby · Christopher N. Johnson · Sarah Legge

Received: 22 May 2019 / Accepted: 8 November 2019
© Springer Nature Switzerland AG 2019

Abstract The impacts of invasive predators can be amplified by high densities of invasive prey species. In Australia, hyper abundant rabbit populations lead to high densities of feral cats and correspondingly high impact of cats on native species, especially small mammals. Therefore, it would be expected 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. Our aim was to understand the short-term effects of an experimental reduction of rabbit abundance on feral cats and their small-mammal prey in arid South Australia. We reduced the rabbit population in a 37 km² experimental enclosure by ~ 80%, while monitoring an

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

H. McGregor (✉) · C. N. Johnson · S. Legge
National Environmental Science Program Threatened Species Recovery Hub, Centre for Biodiversity and 9 Conservation Science, University of Queensland, St Lucia, QLD 4075, Australia
e-mail: hugh.mcgregor@utas.edu.au

H. McGregor · C. N. Johnson
School of Natural Sciences, University of Tasmania, Private Bag 55, Hobart, TAS 7001, Australia

H. McGregor · K. Moseby
Arid Recovery, P.O. Box 147, Roxby Downs 5725, Australia

K. Moseby
University of New South Wales, Sydney 2052, Australia

Keywords Prey switching · Animal-borne video · Diet · Mesopredator · Introduced predator · Invasive species · Wildlife

Introduction

Invasive predators are a major threat to biodiversity worldwide, often having greater impacts on prey than do native predators (Paolucci et al. 2013). This

disparity can be due to several factors, 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 traits that give some invasive predators an advantage (Vermeij 1991; Webb 1985), or anthropogenic disturbances that shift habitats or communities to states that favour invasive predators. The latter factor may be especially relevant to the biological invasions accompanying European colonisation across the world over the last 400 years, which has 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 hyperpredation on native prey (Abrams et al. 1998; Courchamp et al. 2000).

In Australia, invasive feral cats *Felis catus* and red foxes *Vulpes vulpes* threaten many species of native wildlife, especially native mammals between 35 and 5500 g in body mass (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 1996), coinciding with the regions where densities of the invasive European rabbit *Oryctolagus cuniculus* have historically been highest. At least part of the 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, 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. 1992; Pedler et al. 2016). Such control could be in the form of direct suppression (for example, by ripping rabbit warrens or poison-baiting) or the introduction of bio-control agents such as Rabbit Haemorrhagic Disease Virus (RHDV).

Reducing the population density of an invasive predator by manipulating populations of invasive prey could reduce the intensity of predation on alternative native prey (Courchamp et al. 2000). However, after a decline of invasive prey the predators could switch to native 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 population in 1995/96, the resulting epidemic caused widespread decline of rabbits, and associated declines in populations of feral

cats and red foxes. During this period, studies investigating the diets of cats and foxes through scat and stomach contents found that the 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 populations of native prey is disputed (Doherty et al. 2015a; Mutze 2017), mainly because it 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. For example, Pedler et al. (2016) reports how four threatened native mammals have increased in range in South Australia, which they attribute to RHDV.

Our understanding of the impacts on native prey of prey-switching by feral cats and foxes is limited by the fact that to date all evidence of the phenomenon comes from analysis of diet 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 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 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. 2015; Short et al. 2002). Such surplus killing makes it possible that kill rates per predator may decline following a decline in primary prey, but that intake rates remain the same because predators are eating more of the native animals they have killed. Third, differentiating between freshly-killed prey and carrion is unreliable from scat and stomach analysis. This potentially confounding factor is especially important in situations where large amounts of carrion are available to predators, e.g. following pest culls. A more detailed understanding of how cats respond when their primary prey populations are reduced is essential to assess the effects on native prey of prey-switching.

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 this effect 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 and their potential impacts on native wildlife, we conducted a Before/After/Control/Impact study of feral cats and their prey during a population reduction of rabbits. We used this design to answer the following questions about the effects of abrupt declines in rabbits: (1) does cat activity, body condition and survival decrease? (2) do cats prey-switch, and do their diets and kill-rates on native wildlife increase? and (3) does abundance of alternative prey such as native small mammals decline?

Methods

Study area

Our research was conducted in central South Australia, in and around the 123 km² Arid Recovery Reserve (30° 29' S, 136° 53' E). Approximately 60 km² of this reserve is surrounded by a feral-proof fence completed in 2001, whilst the remaining 62 km² consists of two fenced areas created by 2008 for the purposes of landscape-scale research. The area has an average annual rainfall of 170 ml (Olympic Dam Aerodrome, BOM), and is mostly characterized by swales containing scattered small shrubs, dissected by longitudinal sand-dunes and some ephemeral creek lines. We worked in the 'Dingo Paddock', a 37-km² fenced area with a 1.6 m high feral-proof fence constructed using 40 mm gauge wire and a floppy top that curves outwards (Moseby et al. 2012). This fence prevented adult rabbits, dingoes, cats and foxes from entering the paddock, but would not prevent feral cats already resident from exiting. The southern boundary of the Dingo Paddock abuts the rest of the Arid Recovery reserve, where 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. 2019). During the study, there was one dingo present in the Dingo Paddock, and no known foxes or quolls. The surrounding area was used as a control for

the study, mostly on the neighboring Stuart Creek Mulgaria Stations (Fig. 1). These areas contain similar types and proportions of habitats, but they are also subject to cattle grazing and have greater detection rates of dingoes, kangaroos and emus (Moseby et al. 2018).

Study design

We conducted a Before/After/Control/Impact study of feral cats and their prey during a population reduction of rabbits. In late February 2017, 2215 rabbits were removed from the Dingo Paddock over a 14-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 3 months prior to the reduction effort and for 3 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 distance from the track as well as the position of the vehicle along transect. Densities of rabbits were estimated using 'Rdistance'. The area was divided into dune and swale zones, densities were estimated separately for the sections of transects passing through these zones. The total population of rabbits was estimated by multiplying the habitat-specific densities by the total area of each zone in each of the rabbit reduction and control areas. We then multiplied these estimates by 1.3 to account for animals missed that we determined using a thermal camera. This was based on five nights of spotlighting where temperatures were below 20 °C, where 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. This person typically recorded an average of 31% more (SE = 4%).

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

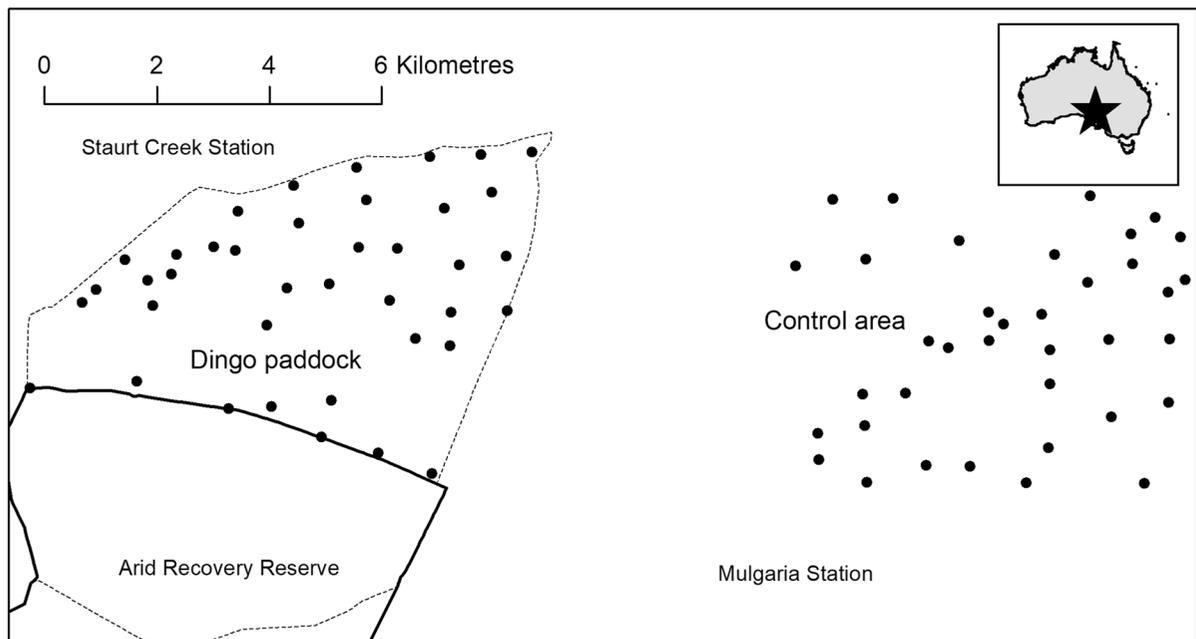


Fig. 1 Map of the study area, showing the Dingo Paddock where experimental removal of rabbits was conducted, the adjoining fenced reserve, and the area outside the reserve used

200 m 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.

Changes in activity between the two time periods were examined separately for cats, rabbits and native mammals. We ran a candidate set of generalized linear mixed models encompassing our Before/After/Control/Impact treatments, including a null model, session, area, session-by-area interaction terms, and another three again with the habitat variable (dune, creek-line and swale). These assumed a Poisson error distribution, and individual transect was set as the random term. We compared these seven models using the Akaike Information Criterion for small sample sizes (AICc) and selected the model with the lowest AICc score (Burnham and Anderson 1998).

Cat body condition and survival

Cats were captured in the Dingo Paddock from August 2016 to February 2017 using cage traps and soft-jaw leg traps (Victor #1.5) with cat urine as lure. Each cat

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

was fitted with a collar containing a VHF beacon ($n = 30$), and some were also fitted with a video collar (discussed in further detail below). Cats were recaptured at intervals of 3–12 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 it to run out into the trap. Once captured, cats were placed in a dark bag and processed without sedation. We measured weight and condition (1-5 scale, where 1 denotes close to death and severely malnourished, 5 denotes excellent condition with hip bones and backbone hard to feel through the thick layer of fat). We also collared six cats in the control area. 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 area, we instead measured the condition of all cats euthanased during normal cat-control operations within 20 km 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 reduction effort using a generalized linear model.

Survival was analysed for 29 of the 30 cats that were VHF-tracked. The fate of only one cat was

unknown, but we believe this cat left the Dingo Paddock as there was still 3 months 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 influencing cat survival, we used Cox Survival analysis with log-linear distribution and the ‘survival’ library in R (Therneau 2014). We considered the importance to different variables using an AICc model averaging framework (Burnham and Anderson 1998), and those with. Models were evaluated using AICc. Explanatory variables considered were pre- versus post-reduction, sex, body weight, and whether individual cats appeared aware of a food-source in the south of the rabbit reduction area; where small mammals moved through the fence (Moseby et al. 2019). This was determined from five remote cameras (Reconyx HC600, Wisconsin, USA) set along this boundary for the entire study period, and each collared cat was individually identified.

Prey selection by cats

We measured changes in cat diet and assumed hunger by analyzing scat contents, deploying animal-borne video collars and measuring uptake of supplementary food. For analysis of scat content, we collected scats both inside the Dingo Paddock and in the neighboring control area before and after the rabbit reduction effort. All scats were placed in a paper bag, and the location, date, and likely age of scat recorded. We also collected scat from cats killed in the control area that had full colons. Scat was dried and sent for analysis to Georgeanna Story (Scats About Pty Ltd, Majors Creek NSW), who identified vertebrate species, estimated the count of small-mammal individuals and recorded number of invertebrates. We used an analysis of variance test to compare the presence of rabbit in scats, the count of small mammals (all species combined), and the number of all other prey species found in scats (hereafter alternative prey) between each treatment (experimental/control) and time period (pre- and post-reduction). We then conducted a Tukey post hoc test with a 0.95% cutoff, and only consider a significant change if there was a difference between before/after in the rabbit reduction paddock and not in the control area.

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 (Loyd et al. 2013; McGregor et al. 2015). We deployed these 27 times throughout the entire study period, with the aim of obtaining similar amounts of footage before and after the rabbit reduction. Collars were made with modified GoPro Hero 3 White cameras (GoPro Inc, San Mateo, California, USA), with extra infra-red LEDs placed next to the lens (920 nm), VHF beacon (Sirtrack, Havelock, New Zealand), additional batteries (Lithium-ion 1300 mha), and a delay timer created with Arduino Atiny85 chips (ATMEL, San Jose, California, USA) that would turn the camera on 11 h post release. After parts were compiled, they were coated in epoxy resin (SC651, Solid Solutions, Bentleigh East, Australia). Working deployments obtained 6–10 h of footage. All footage was reviewed, and behavior was categorized into one of five classes (still, walking, grooming, investigating a rabbit warren, hunting).

With data from video-collars on cats, we compared hunting rates of cats before and after the experimental rabbit control. We calculated event rates per hour for rabbits, small mammals and ‘alternative’ foods (carrion, insects, small lizards). Each camera deployment was treated as a sample unit. We only used deployments that were active for more than an hour to estimate kill rates for cats, as deployments with less than that typically just small movements between sleeping. Rates of hunting on small mammals and alternative prey were compared 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 rabbit warrens as an index of hunting of rabbits by cats before and after the rabbit reduction.

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. We used skinless beef Chevaps sausages left in the sun for 6 h, which increased the smell. Sausages were placed at 20 sites in the experimental rabbit reduction area and 20 in the control area at three time points: 3 months before, during, and 3 weeks after rabbit reduction. For each cat detected on camera when a sausage was available, we recorded whether it ate or ignored it. Cameras were deployed until we obtained at least 15 instances of a cat interacting with a sausage in each of the rabbit

reduction and control areas. Outside of the rabbit reduction area, we often needed to rebait cameras repeatedly until this sample size was reached. The fate of the 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.

Results

Effectiveness of rabbit reduction

Rabbit reduction was undertaken in the study area for 14 days in February/March 2017, removing 2215 rabbits. Distance sampling based on spotlighting counts of rabbits estimated a population of 2756 (95% CI = 2430–3082, or 76/km²) in the paddock before removal, and 448 (95% CI = 298–598, or 12/km²) afterwards. No decline in estimated density was detected in the control area (21/km² before, 26/km² after). The distance sampling model was 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 was best explained by a model including a habitat variable, with tracks being higher on dunes and lower in swales, and also included the interaction between treatment area and period (Fig. 2, Table 1). This model showed a 86% drop of rabbit activity in the treatment area following the experimental rabbit control, but no change in the nearby control area.

Cat activity, body condition and survival

Cat activity on track transects was best explained by a model containing session by paddock (delta AICc 5.93 lower than next model, 14.72 from null, and AICc weight of 0.93, Table 1). In this model, cat activity was initially much higher in the Dingo Paddock (~ fivefold), but the track counts of cats dropped by 32% after the rabbit reduction (95% CI = 20–45%), and slightly increased in the control area (Fig. 2). No other mesopredator (i.e. fox or quoll) was detected inside or outside, and dingoes were detected on 6% of transects inside and 15% of transects outside. Condition of captured cats declined in the experimental area following rabbit reduction (Fig. 3), but did not change

in the control area ($t = 4.63$, $P < 0.001$). During the radio-tracking period before the rabbit reduction two collared cats were found dead, yet both had gained weight since original capture and were in good condition. Of 21 cats that were collared at the time of the reduction, nine were found dead within 5 weeks. Each of these cats was in poor condition and had lost weight since initial capture. A further 7 cats were caught post rabbit reduction and were all in poor to average health. One radio-collared cat was never detected after the rabbit reduction and probably left the study area. Survival analysis of radio-collared cats estimated a 24-fold decrease in weekly survival probability following rabbit reduction (95% confidence range = 4–156). The most parsimonious model included which cats visited the southern boundary of the study area (Fig. 4, Table 2), 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).

Native rodent activity

Activity of native rodents (principally *Notomys alexis* and *Pseudomys australis*) on the track transects was best described using a model that included an interaction term of treatment and before/after rabbit reduction (Fig. 2), and habitat (AICc delta 7.6 lower than next model, 1058 lower than null, AICc weight = 0.98, Table 1). In this model, activity was initially higher in the experimental area [23 tracks/200 m, 95% CI = 14–32] than the control area (9.5, 95% CI = 5–14); activity declined in both areas after rabbit reduction (– 0.49 times reduction, 95% CI = – 0.35 to – 0.63), but the rate of decline was greater in the experimental area (– 2.01 times reduction, 95% CI = – 1.76 to – 2.26).

Cat diet and hunting behaviour

From the 64 cat scats collected, those in the rabbit reduction area contained significantly (i.e. $P < 0.05$) less rabbit after the rabbit reduction (though there was also a non-significant decrease in outside of a similar magnitude), but significantly more alternative prey such as reptiles, insects and birds (Table 3). No significant change was detected in frequency of small mammals (rodents and small dasyurids) (Table 3). From 27 deployments of video collars on 18 cats,

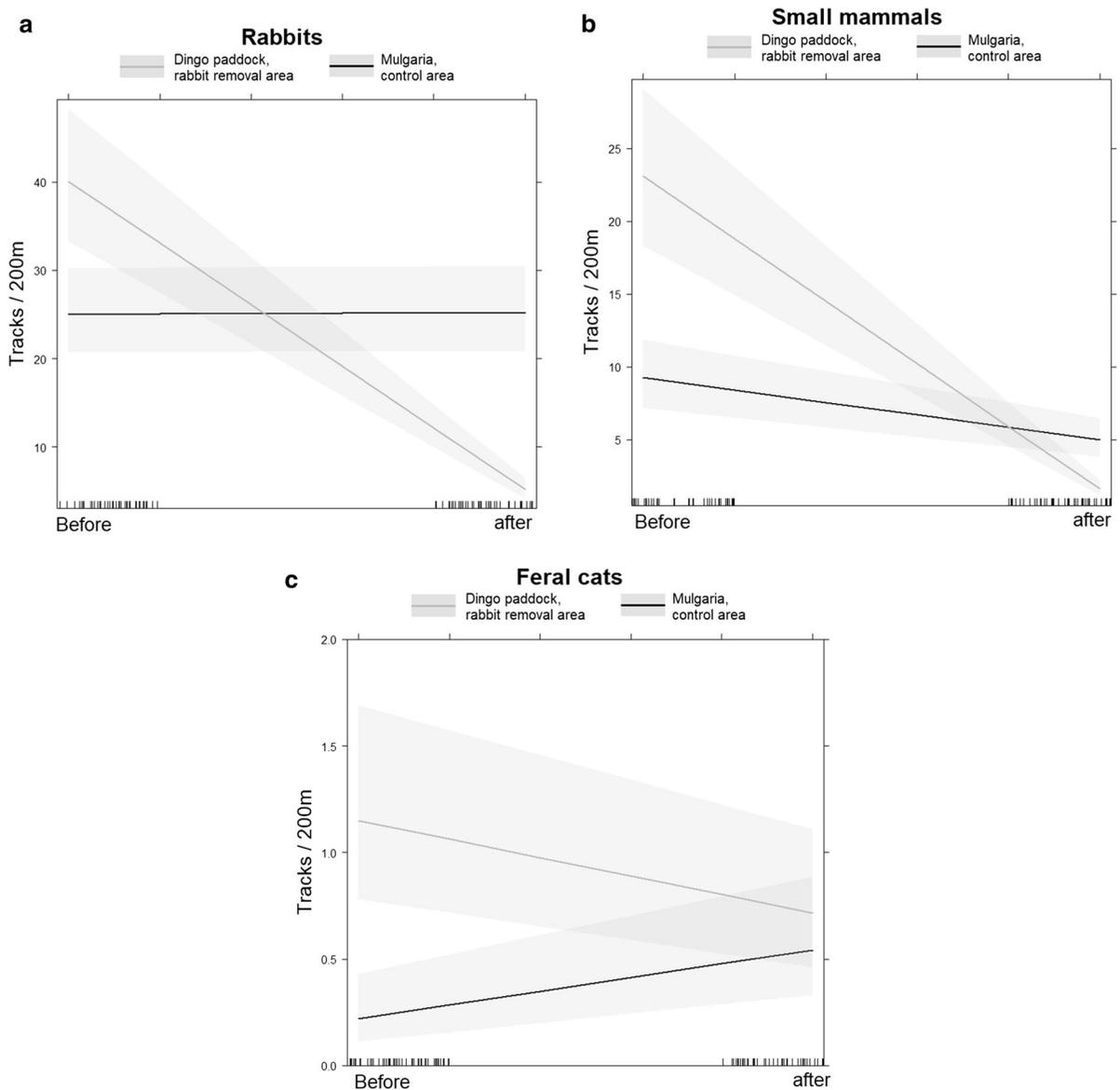


Fig. 2 Changes in track counts of rabbits, small mammals and feral cats inside the Dingo Paddock (rabbit removal area) and Mulgaria (nearby control zone) before and after a major rabbit

reduction effort was conducted in the Dingo Paddock. Grey shading indicates 95% confidence intervals

cameras worked on 22, recording a total of 104 h of footage. However, only 15 of these deployments contained footage where cats were active for over an hour. In total, we recorded 22 h of cat activity before the rabbit reduction and 33 h after. After the rabbit reduction there were significantly more instances of cats eating carrion and small prey items, but no difference in the take of small mammals (Table 4). The number of rabbit warrens visited per hour of cat

activity was non-significantly greater before the rabbit reduction, and this difference was largely driven by footage from one cat who visited 11 warrens in an hour (Table 4). 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

Table 1 Model selection tables for track counts of the different species groups before and after rabbit reduction, including variables of which experimental area (area), before or after rabbit reduction (session), and whether transect was in dune, swale or creekline (habitat)

Species	Model	df	LogLik	AICc	Delta	Weight
Rabbits	Area × session + habitat	7	− 873.6	1762	0	1
	Area × session	5	− 890.1	1790.6	28.6	0
	Session + habitat	5	− 1290.8	2592.1	830	0
	Session	3	− 1307.1	2620.3	858.2	0
	Area + habitat	5	− 1620.9	3252.2	1490.2	0
	Null	2	− 1637.2	3278.5	1516.4	0
	Area	3	− 1637.1	3280.4	1518.4	0
Native mice	Area × session + habitat	7	− 658.3	1331.3	0	0.978
	Area × session	5	− 664.3	1338.9	7.6	0.022
	Session + habitat	5	− 797	1604.4	273.1	0
	Session	3	− 802.5	1611.1	279.8	0
	Area + habitat	5	− 1181.8	2374	1042.7	0
	Area	3	− 1188.2	2382.5	1051.2	0
	Null	2	− 1192.7	2389.5	1058.2	0
Cats	Area × session + habitat	7	− 185.8	386.5	0	0.932
	Area	3	− 193.1	392.4	5.9	0.048
	Area + habitat	5	− 191.9	394.2	7.8	0.019
	Null	2	− 198.6	401.2	14.7	0.001
	Session	3	− 198.4	403	16.5	0
	Area × session	4	− 197.8	403.8	17.3	0
	Session + habitat	5	− 197	404.4	17.9	0

geckos and one *Nephrurus* spp. (Fig. 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. There were no instances where a cat ate a sausage in the control area at any time (n = 22 before, 19 during, 16 after). In the Dingo Paddock, no cat ate a sausage before the rabbit reduction (n = 20 before, 26 during, 17 after), yet there was significant increase afterwards with 41% of cats eating one ($z = 2.89$, $P = 0.004$).

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 2 months following the rabbit decline, and those that survived hunted in an area with a replenishing prey source; small mammals entering the rabbit reduction 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.

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 (Doherty et al. 2015a; Wysong et al. 2019), though similar to those conducted prior to RDHV (Holden and Mutze 2002; Molsher et al. 1999). The rabbit density in the study area was very high by contemporary standards (Pedler et al. 2016), and likely supported high levels of cat density. However, at a continental scale rabbits are not necessarily preferred prey of feral cats, and most studies report greatest preference for small mammals between 35 and 400 g (Doherty et al. 2015a; Radford et al. 2018). Rabbits are likely to be harder to hunt and kill than are many other prey species due to their size (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.

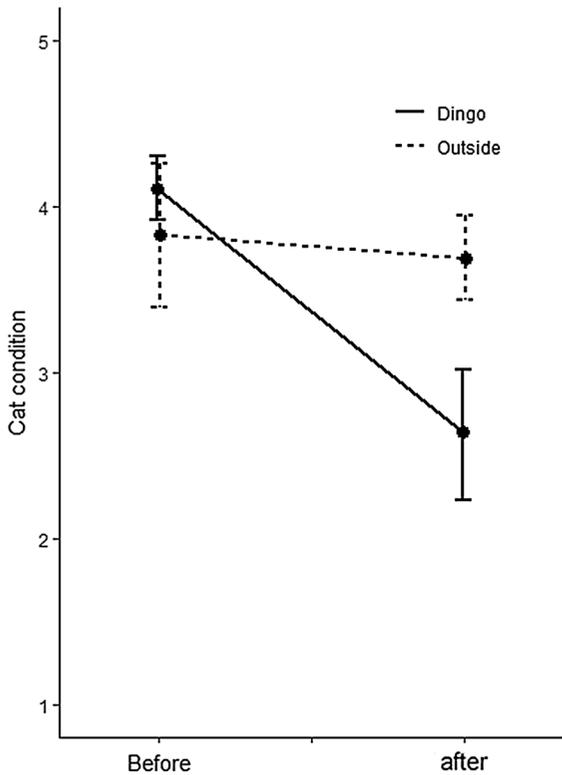


Fig. 3 Changes in cat condition before and after the rabbit reduction effort within Dingo Paddock experimental, compared to nearby control area

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 similar prey-switching from scat or stomach analysis (Delibes-Mateos et al. 2008; Norbury et al. 2013; Yip et al. 2015), and we further corroborate this behavior using video collars to show there is also an increase in kills per hour.

Prey switching by feral cats appears to have caused a decline in activity of small mammals (mostly *N. alexis* and *P. australis*), suggesting the potential to threaten other native mammals in similar circumstances. However, complicating this interpretation was small mammals also declined in the control area (though not as pronounced), and we did not find evidence of increased hunting from either scat analysis or animal-borne video. One possible explanation is that cats did increase their targeting of small mammals, but their incidence in the diet didn't change as small mammals became increasingly rare, as Read and Bowen (2001) and Saunders et al. (2004) found with

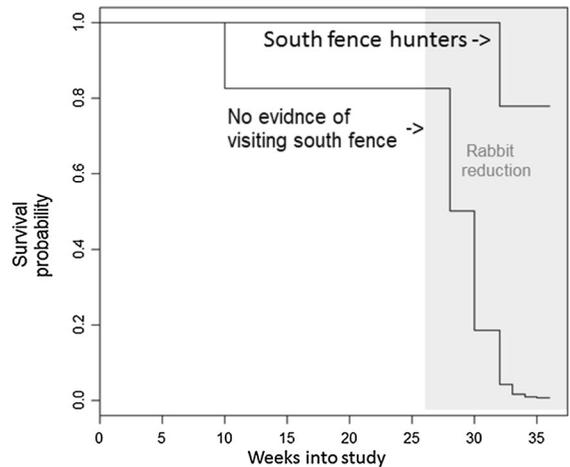


Fig. 4 Survival of cats in the experimental area following rabbit reduction. ‘South fence hunters’ were those that were detected on remote cameras on the southern boundary of the study paddock, where availability of small mammals would have been greatest after the rabbit reduction effort. This southern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

Table 2 Model selection tables for factors affecting feral cat survival after a reduction in rabbit density

Model	df	LogLik	AICc	Delta	Weight
Fence	1	- 24.9	52.3	0	0.932
Global	3	- 24.3	58	5.7	0.054
Weight	1	- 29.7	61.8	9.6	0.008
Sex	1	- 29.9	62.3	10	0.006

rabbits. Another explanation could be cats always prefer small mammals and there was no change before and after, but the high abundance of cats with the rabbit reduction area caused a greater rate of attrition of small mammals than outside in the 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 mammals, we were not able to demonstrate the underlying mechanistic process.

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 likelihood of cats eating novel food sources and carrion, as demonstrated here. But

Table 3 Count of prey in scats collected from cats before and after the rabbit reduction in the Dingo Paddock, and a nearby control area where rabbit populations remained stable over the same time period

	Dingo Paddock		Outside		Tukey post hoc B/A Dingo Paddock	<i>P</i> values B/A outside
	Before	After	Before	After		
Scats (n)	26	12	14	12		
Rabbits	0.81	0.42	0.57	0.25	0.049*	0.286
Alternative prey ^a	0.81	2.67	0.79	1.42	< 0.001*	0.464
Small mammals ^b	0.88	0.58	0.57	1.17	0.678	0.358

Also reported is statistical difference using Tukey post hoc tests between before and after (B/A) in the Dingo Paddock and outside, and changes considered significant (denoted *) if $P < 0.05$ in the former but not the latter

^aIncludes birds, reptiles and insects

^bIncludes rodents and small dasyurids

Table 4 Hunting and food consumption events by feral cats witnessed on animal-borne video-collars before and after a major rabbit reduction effort, and changes considered significant (denoted *) if $P < 0.05$

	Events witnessed		Events per hour of activity		<i>t</i>	<i>P</i>
	Before	After	Before	After		
Rabbits	2	0	0.12	0	–	–
Small mammals	5	3	0.19	0.2	0.13	0.889
Alternative prey ^a	2	30	0.11	0.37	– 2.7	0.016*
Carrion	0	5	0	0.13	– 2.46	0.028*
Investigate rabbit warren	37	22	3.56	0.98	0.25	0.807

^aIncludes reptiles, insects and small unidentified items consumed

this prey switching also means cats would be more susceptible to control techniques that rely on hunger, such as poison baiting or trapping with food lures. This greater susceptibility has also been shown by Christensen et al. (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 suggest conservation managers aiming to reduce cat populations should take advantage of declines in rabbit abundance by targeting baiting programs to such times. Not only could integrated control efforts 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 prior to control would likely improve the uptake of control methods or help naturally reduce cat abundance.

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 humidity around the time of the rabbit reduction, potentially giving cats a greater need for energy and moisture. Cats that did not hunt near the boundary of the Arid Recovery Reserve were not sustained on the alternative prey available. Given the potential period for prey-switching is immediate, managers need to be prepared to react quickly to protect vulnerable 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.

Our experimental study supports the descriptive research of the aftermath of the original calicivirus release in 1995–1996, which resulted in an increase in occurrence of alternative prey in diet of feral predators (Molsher et al. 1999; Mutze et al. 1998; Read and

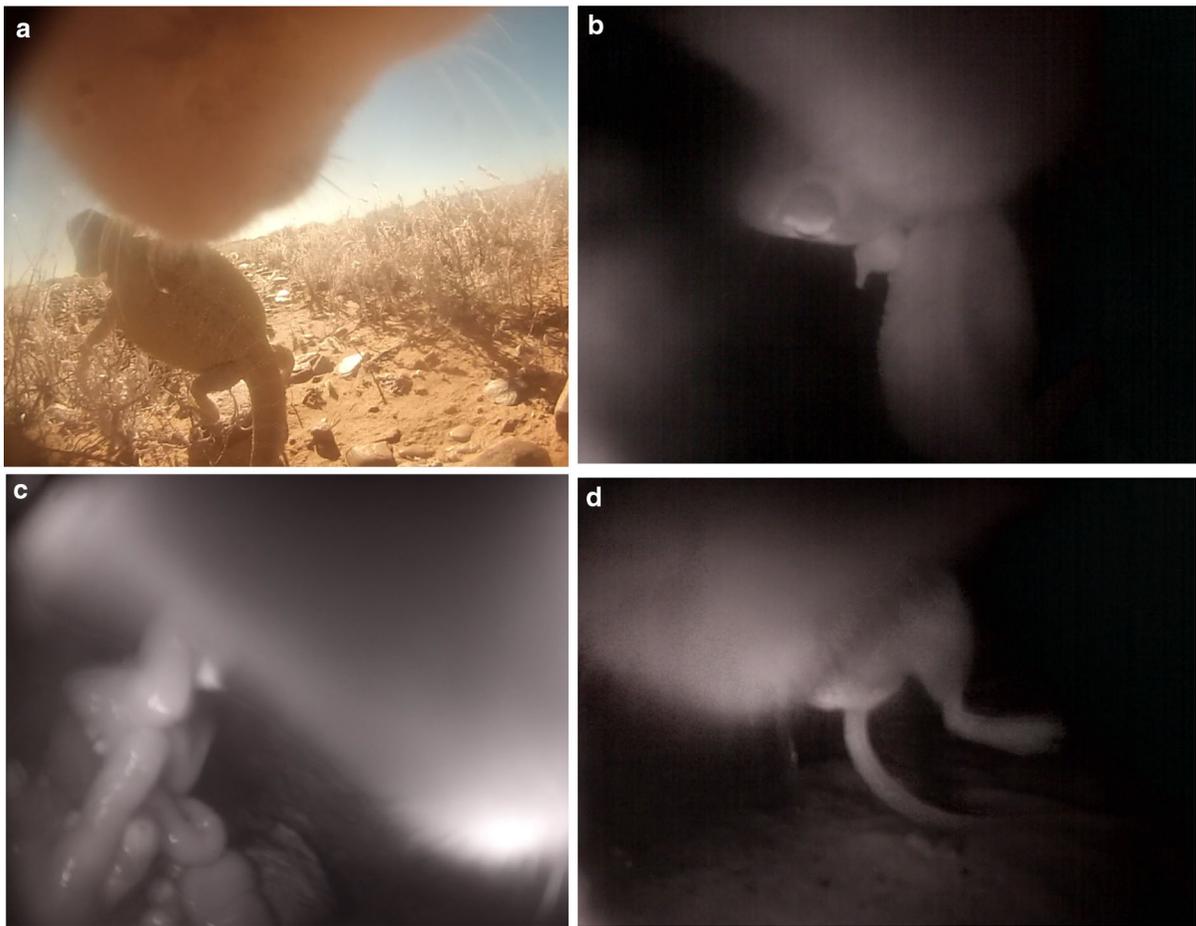


Fig. 5 Images from video-collars deployed on cats, of a cat investigating but not eating a bearded dragon (**a**), eating a *Nephurus* spp. (**b**), consuming the intestines of a rabbit (**c**), and catching a spinifex hopping mouse (**d**)

Bowen 2001), but an overall decrease in cat density that would ultimately be beneficial for many 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. 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 open landscape in which control areas could be quickly reinvaded by dispersing animals. The results of this study might not be replicated in an open landscape if conducted at the same scale. Even if inherent carrying capacity is locally reduced, predators from outside would continue to come in looking for food. However, if the scale of the rabbit decline and resultant reduction in predator density is very large, such as with

calicivirus releases, then even immigration into 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 non-native 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; Norbury et al. 2013). When those predators take relatively fewer native prey per capita but predator densities are elevated, then the cumulative predation toll on native species would

exceed that if predators are at lower density. Even though individual cats consumed more rabbits and less native prey before the rabbit reduction, it is unlikely that maintaining a 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 long-term benefits, whilst impacts of prey-switching would be short-term and potentially mitigated. If we can manage processes that interact synergistically with feral predators, we should have a greater chance of reducing the overall impact of invasive predators.

Acknowledgements Arid Recovery hosted and supported this project. They are an independent conservation and research initiative supported by BHP, The University of Adelaide, Bush Heritage Australia and The South Australian Department for Environment and Water. The rabbit removal effort was conducted by Frank Bernhardt (Bernhardt's Pest & Weed Control). Zac Richardson assisted with field data collection. Menna Jones, Greg Mutze, David Peacock, and Reece Pedler assisted with project development. Katherine Tuft and Catherine Lynch provided logistical support. Two anonymous reviewers provided expert advice for improving this manuscript. H McG and SL are supported by the National Environmental Program's Threatened Species Recovery Hub.

Authors' contribution All authors conceived the ideas and designed methodology; HM collected and analyzed the data; HM led writing of the manuscript; and all authors contributed critically to the drafts and gave final approval.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Data collection fulfilled all legal requirements in Australia, and methods were approved by University of Tasmania Animal Ethics Committee (A0015720).

References

- Abrams PA, Holt RD, Roth JD (1998) Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* 79(1):201–212
- Algar D, Angus GJ, Williams MR, Mellican AE (2007) Influence of bait type, weather and prey abundance on bait uptake by feral cats (*Felis catus*) on Peron Peninsula, Western Australia. *Conserv Sci West Aust* 6(1):109–149
- Burbidge AA, Manly BFJ (2002) Mammal extinctions on Australian islands: causes and conservation implications. *J Biogeogr* 29(4):465–473
- Burnham KP, Anderson DR (1998) Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin
- Christensen PE, Ward BG, Sims C (2013) Predicting bait uptake by feral cats, *Felis catus*, in semi-arid environments. *Ecol Manag Restor* 14(1):47–53
- Courchamp F, Langlais M, Sugihara G (2000) Rabbits killing birds: modelling the hyperpredation process. *J Anim Ecol* 69(1):154–164
- Delibes-Mateos M, De Simon JF, Villafuerte R, Ferreras P (2008) Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. *Eur J Wildl Res* 54(1):71–78
- Dickman CR, Newsome TM (2015) Individual hunting behaviour and prey specialisation in the house cat *Felis catus*: implications for conservation and management. *Appl Anim Behav Sci* 173:76–87
- Doherty T, Davis RA, Etten EJB, Algar D, Collier N, Dickman CR, Edwards GP, Masters P, Palmer R, Robinson S (2015a) A continental-scale analysis of feral cat diet in Australia. *J Biogeogr* 42(5):964–975
- Doherty TS, Dickman CR, Nimmo DG, Ritchie EG (2015b) Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biol Conserv* 190:60–68
- Griffin AS, Blumstein DT, Evans CS (2000) Training captive-bred or translocated animals to avoid predators. *Conserv Biol* 14(5):1317–1326
- Holden C, Mutze G (2002) Impact of rabbit haemorrhagic disease on introduced predators in the Flinders Ranges, South Australia. *Wildl Res* 29(6):615–626
- Jones E, Coman B (1981) Ecology of the Feral Cat, *Felis catus* (L.), in South-Eastern Australia I. Diet. *Wildl Res* 8(3):537–547
- Kruuk H (1972) Surplus killing by carnivores. *J Zool* 166(2):233–244
- Loyd KAT, Hernandez SM, Carroll JP, Abernathy KJ, Marshall GJ (2013) Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biol Conserv* 160:183–189
- McGregor HW, Legge S, Jones ME, Johnson CN (2015) Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE* 10(8):e0133915
- Molsher R, Newsome A, Dickman CR (1999) Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildl Res* 26(5):593–607
- Moseby K, Read J, Gee P, Gee I (1998) A study of the Davenport Range black-footed rock wallaby colony and possible threatening processes. Final report to Wildlife Conservation Fund. Department for Environment and Heritage, Adelaide
- Moseby KE, Neilly H, Read JL, Crisp HA (2012) Interactions between a top order predator and exotic mesopredators in the Australian rangelands. *Int J Ecol* 2012:1–15
- Moseby KE, Peacock DE, Read JL (2015) Catastrophic cat predation: a call for predator profiling in wildlife protection programs. *Biol Conserv* 191:331–340
- Moseby KE, Blumstein DT, Letnic M (2016) Harnessing natural selection to tackle the problem of prey naïveté. *Evol Appl* 9(2):334–343

- Moseby K, Crowther M, Letnic M (2018) Ecological role of an apex predator revealed by a reintroduction experiment and Bayesian statistics. *Ecosystems* 2018:1–13
- Moseby K, McGregor H, Hill BM, Read J (2019) Exploring the internal and external wildlife gradients created by conservation fences. *Conserv Biol* 2019:1–12
- Murphy EC, Keedwell RJ, Brown KP, Westbrooke I (2005) Diet of mammalian predators in braided river beds in the central South Island, New Zealand. *Wildl Res* 31(6):631–638
- Mutze G (2017) Continental-scale analysis of feral cat diet in Australia, prey-switching and the risk: benefit of rabbit control. *J Biogeogr* 44(7):1679–1681
- Mutze G, Cooke B, Alexander P (1998) The initial impact of rabbit hemorrhagic disease on European rabbit populations in South Australia. *J Wildl Dis* 34(2):221–227
- Norbury G, Byrom A, Pech R, Smith J, Clarke D, Anderson D, Forrester G (2013) Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. *Ecol Appl* 23(7):1707–1721
- Paolucci EM, MacIsaac HJ, Ricciardi A (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Divers Distrib* 19(8):988–995
- Pech RP, Hood G (1998) Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. *J Appl Ecol* 35(3):434–453
- Pech RP, Sinclair A, Newsome A, Catling P (1992) Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia* 89(1):102–112
- Pedler RD, Brandle R, Read JL, Southgate R, Bird P, Moseby KE (2016) Rabbit biocontrol and landscape-scale recovery of threatened desert mammals. *Conserv Biol* 30:774–782
- Radford JQ, Woinarski JCZ, Legge S, Baseler M, Bentley J, Burbidge AA, Bode M, Copley P, Dexter N, Dickman CR, Gillespie G, Hill B, Johnson CN, Kanowski J, Latch P, Letnic M, Manning A, Menkhorst P, Mitchell N, Morris K, Moseby K, Page M, Ringma J (2018) Degrees of population-level susceptibility of Australian terrestrial non-volant mammal species to predation by the introduced red fox (*Vulpes vulpes*) and feral cat (*Felis catus*). *Wildl Res* 45(7):645–657
- Read J, Bowen Z (2001) Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildl Res* 28(2):195–203
- Saunders G, Berghout M, Kay B, Triggs B, Ven RVD, Winstanley R (2004) The diet of foxes *Vulpes vulpes* in south-eastern Australia and the potential effects of rabbit haemorrhagic disease. *Wildl Res* 31(1):13–18
- Scroggie MP, Forsyth DM, McPhee SR, Matthews J, Stuart IG, Stamation KA, Lindeman M, Ramsey DS (2018) Invasive prey controlling invasive predators? European rabbit abundance does not determine red fox population dynamics. *J Appl Ecol* 55(6):2621–2631
- Short J, Kinnear JE, Robley A (2002) Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species? *Biol Conserv* 103(3):283–301
- Smith AP, Quin DG (1996) Patterns and causes of extinction and decline in Australian conilurine rodents. *Biol Conserv* 77(2):243–267
- Therneau, T.M. (2014) A package for survival analysis in R package
- Vermeij GJ (1991) When biotas meet: understanding biotic interchange. *Science* 253(5024):1099–1104
- Webb SD (1985) The great American biotic interchange. Springer, Berlin, pp 357–386
- Woinarski JCZ, Burbidge AA, Harrison PL (2015) Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proc Natl Acad Sci* 112(15):4531–4540
- Wysong ML, Tulloch AIT, Valentine LE, Hobbs RJ, Morris K, Ritchie EG (2019) The truth about cats and dogs: assessment of apex- and mesopredator diets improves with reduced observer uncertainty. *J Mamm* 100(2):410–422
- Yip SJ, Rich M-A, Dickman CR (2015) Diet of the feral cat, *Felis catus*, in central Australian grassland habitats during population cycles of its principal prey. *Mamm Res* 60(1):39–50

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.