

McGregor H., Read J., Johnson C.N., Legge S., Hill B., Moseby K. (2020) Edge effects created by fenced conservation reserves benefit an invasive mesopredator. *Wildlife Research*, Vol. 47, Iss. 8, Pp 677-685.

DOI: <https://doi.org/10.1071/WR19181>

Edge effects created by fenced conservation reserves benefit an invasive mesopredator

Hugh McGregor, John Read, Christopher N. Johnson, Sarah Legge, Brydie Hill and Katherine Moseby

Abstract

Context: Fenced reserves from which invasive predators are removed are increasingly used as a conservation management tool, because they provide safe havens for susceptible threatened species, and create dense populations of native wildlife that could act as a source population for recolonising the surrounding landscape. However, the latter effect might also act as a food source, and promote high densities of invasive predators on the edges of such reserves.

Aims: Our study aimed to determine whether activity of the feral cat is greater around the edges of a fenced conservation reserve, Arid Recovery, in northern South Australia. This reserve has abundant native rodents that move through the fence into the surrounding landscape.

Methods: We investigated (1) whether feral cats were increasingly likely to be detected on track transects closer to the fence over time as populations of native rodents increased inside the reserve, (2) whether native rodents were more likely to be found in the stomachs of cats caught close to the reserve edge, and (3) whether individual cats selectively hunted on the reserve fence compared with two other similar fences, on the basis of GPS movement data.

Key results: We found that (1) detection rates of feral cats on the edges of a fenced reserve increased through time as populations of native rodents increased inside the reserve, (2) native rodents were far more likely to be found in the stomach of cats collected at the reserve edge than in the stomachs of cats far from the reserve edge, and (3) GPS tracking of cat movements showed a selection for the reserve fence edge, but not for similar fences away from the reserve.

Conclusions: Invasive predators such as feral cats are able to focus their movements and activity to where prey availability is greatest, including the edges of fenced conservation reserves. This limits the capacity of reserves to function as source areas from which animals can recolonise the surrounding landscape, and increases predation pressure on populations of other species living on the reserve edge.

Implications: Managers of fenced conservation reserves should be aware that increased predator control may be critical for offsetting the elevated impacts of feral cats attracted to the reserve fence.

Introduction

Invasive predators are a major threat to wildlife in many ecosystems. In Australia and New Zealand, the cat, *Felis catus*, and red fox, *Vulpes vulpes*, have caused many recent extinctions, and continue to threaten biodiversity and prevent recovery of native species ([Holdaway 1999](#); [Woinarski et al. 2015](#)). Fenced reserves from which introduced predators have been removed are increasingly used as a management tool to provide refuge for wildlife ([Hayward and Somers 2012](#)). In Australia, there are currently 17 established fenced havens, with more being under construction ([Legge et al. 2018](#)), and 28 of varying sizes in New Zealand ([Burns et al. 2012](#); [Saunders and Norton 2001](#)). Many populations of species vulnerable to invasive predators are now dependant on these fenced reserves for their survival.

Fenced reserves can benefit conservation in two ways. First, they provide havens for species susceptible to predation by invasive predators, and allow self-sustaining populations to persist in the

absence of landscape-scale solutions to the problem of predation ([Miskelly and Powlesland 2013](#); [Hayward et al. 2015](#); [Kanowski et al. 2018](#)). Second, fenced reserves create dense populations of threatened species that could act as source populations for recolonisation elsewhere (e.g. [Russ and Alcala 2011](#)). Recolonisation could be achieved by managed translocations of animals from reserves into distant or surrounding areas ([Moseby et al. 2011](#); [Hayward et al. 2012](#); [Read et al. 2018](#)), or through free movement of animals across the reserve boundary to the outer edge ([Tanentzap and Lloyd 2017](#)). Free movement could be accomplished either through the provision of one-way gates designed to allow animals to leave, while continuing to prevent entry of predators ([Butler et al. 2019](#)), or by dispersal of animals that are capable of climbing or flying over fences or passing through them ([Tanentzap and Lloyd 2017](#); [Moseby et al. 2019](#)).

The importance of fenced reserves as havens is well documented ([Burns et al. 2012](#); [Legge et al. 2018](#)). However, the value of fenced reserves for recolonisation of surrounding areas is much less clear (but see [Moseby et al. 2019](#)). The primary impediment to such recolonisation is the difficulty in reducing predation pressure in surrounding landscapes to levels that can allow threatened species to establish viable populations. This explains the failure of most managed translocations of threatened species from fenced reserves into surrounding areas ([Moseby et al. 2011](#); [Hayward et al. 2012](#); [Miskelly and Powlesland 2013](#)). Instances where such predation threats have been adequately reduced over the long term are rare, because landscape control of introduced predators (especially feral cats) is notoriously difficult ([Denny and Dickman 2010](#)).

Contrary to their conservation role, fenced reserves may perversely promote high densities of predators in the immediate surrounding area. This effect could be created by several processes. First, the fence itself could funnel predator movements in the same way as linear features such as roads are followed by some mammalian predators ([Loarie et al. 2009](#); [Read and Eldridge 2010](#)). Second, management of fenced reserves often includes predator control immediately outside reserves, with the aim of preventing incursions. This control could create sink populations of predators, in which removal of dominant individuals results in a high influx of dispersing individuals ([Bodey et al. 2011](#); [Lazenby et al. 2014](#)). And third, in cases where species that are susceptible to predation by introduced predators are able to move across reserve boundaries, they might provide a regular supply of prey in the area immediately surrounding the reserve, attracting predators and, thereby, maintaining high levels of predator activity. If any of these processes were operating, they could raise the threat of predation near fenced reserves above that of distant places. Consequently, unless these processes can be addressed, re-establishment of threatened species would be less likely close to fenced reserves.

We investigated these processes at the Arid Recovery reserve in South Australia, a fenced reserve from which invasive animals (cats, rabbits and foxes) have been eradicated. As a result, five threatened mammal species have been successfully established within the fenced area ([Moseby et al. 2011](#)). Ongoing management includes a sustained but relatively low-intensity program of control of invasive predators outside the fenced reserve. As well as acting as a refuge for medium-sized reintroduced mammal species such as bilbies, *Macrotis lagotis*, and burrowing bettongs, *Bettongia lesueur*, the Arid Recovery reserve is a source population of two small rodents able to move into the surrounding landscape ([Moseby et al. 2019](#)). The plains mouse, *Pseudomys australis*, and spinifex hopping mouse, *Notomys alexis*, are both preyed on by feral cats ([Woolley et al. 2019](#)) and exist at a higher abundance inside the reserve ([Moseby et al. 2009a](#)). They are able to pass through the fence to occupy the surrounding landscape ([Moseby et al. 2019](#)). Both species were rare in the region before fence establishment, but gradually increased in abundance inside the reserve after construction ([Read and Cunningham 2010](#)).

A previous study suggested that feral cat activity immediately outside the Arid Recovery reserve fence line is higher than that in the surrounding landscape (Moseby *et al.* 2019). However, the study was conducted only at one point in time, and was unable to investigate the underlying mechanism. Therefore, our study aimed to understand whether cat activity along the fence varies over time, and the possible causes for this. Our hypothesis was that the high activity of feral cats close to the reserve boundary was caused by high availability of native rodents immediately outside the reserve, which, in turn, was due to the elevated population size inside the reserve. We tested this hypothesis in the following ways: first, we examined whether feral cats are more likely to be detected closer to the fence over time because populations of native rodents gradually increase inside the reserve; second, using data from the stomachs of cats killed in the area, we investigated the relationship between the consumption of these rodents by cats and the distance from the reserve edge; and third, we investigated the movements of individual cats in relation to the reserve edge in an area where cats are not being controlled. We did this because the above two investigations were conducted in areas where cats are controlled, so it was not possible to determine whether increased cat activity along the fences was due to selective hunting, or to the demographic effect of a population sink.

Materials and methods

Study area

The Arid Recovery reserve in central South Australia (30°29'S, 136°53'E) is in a semiarid environment with a mean annual rainfall of 160 mm (records from Olympic Dam Aerodrome, www.bom.gov.au/climate/data, accessed 12 October 2019), characterised by clay-swale habitats with longitudinal sand dunes. The reserve is 123 km² in area and includes 60 km² from which European rabbits, *Oryctolagus cuniculus*, red foxes, and feral cats have all been removed. The perimeter of the reserve consists of a floppy-top fence 1.8 m high, with a 30-mm chicken-wire at ground height (Moseby and Read 2006). By 2001, 60 km² of the reserve had been cleared of invasive species and populations of threatened native mammals, including bilbies, burrowing bettongs, western barred bandicoots, *Perameles bougainville*, and stick-nest rats, *Leporillus conditor*, were re-established. By 2008, two extra fenced areas were created on the northern side of reserve, the red lake expansion and dingo paddock (Moseby *et al.* 2012). Both are used for research on predator–prey interactions and contain managed populations of free-living cats and rabbits. Occasional reintroductions of dingoes to these two areas have also been conducted.

Soon after fence construction, small mammals increased in abundance both within the reserve and, to a lesser extent, in the surrounding landscape (Moseby *et al.* 2009a). The species mainly responsible for this increase have been the spinifex hopping mouse, *Notomys alexis*, and a critical weight-range rodent, the plains mouse, *Pseudomys australis*. Both species initially increased gradually, then following major rains in 2010 (402 mm) and 2011 (213 mm), their populations boomed across the entire region (Pedler *et al.* 2016). As the region returned to average rainfall (average 174 mm year⁻¹ between 2012 and 2018), capture rates returned to pre-2010 rates. A study in 2018 confirmed that activity of these small mammals was high in the reserve, lower immediately outside, and declined along a gradient of increasing distance from the perimeter (Moseby *et al.* 2019).

Methods addressing each research question are outlined below.

Are feral cats more likely to be detected closer to the reserve edge over time as populations of native rodents gradually increase inside the reserve?

To measure patterns of cat activity, we used track counts conducted around the Arid Recovery reserve, from 2002, soon after the reserve was created, until 2009, when many threatened mammals had become established in the reserve ([Moseby *et al.* 2009a](#)). Tracks were counted on 200-m transects along the wheel ruts of dirt roads, as per [Moseby and Hill \(2011\)](#) and [Read and Eldridge \(2010\)](#). The start of each transect was marked with a steel pole, so as to ensure locational consistency. Tracks were driven during the afternoon to clear existing sign, and the following morning each transect was visited and the presence of cat tracks was recorded on each segment by a walking observer. Transects were spread throughout the region, at a minimum spacing of 500 m between the transects. Generally, a set of 14–15 transects would be clumped and sampled together, and there were 11 sets over the region ([Fig. 1](#)). There was a total of 160 transects; however, sites were sampled in irregular patterns and 60 sites would typically be sampled every 2 months. In 2005 and 2006, there were monthly samples; so, to reduce bias associated with these years, we excluded odd-numbered months from analysis. This monitoring array was established to measure the response of cats to bait programs and has been published in [Moseby and Hill \(2011\)](#). We re-analysed this dataset because it contains adequate replicates of cat activity at different distances to the Arid Recovery fence ([Fig. 1](#)).

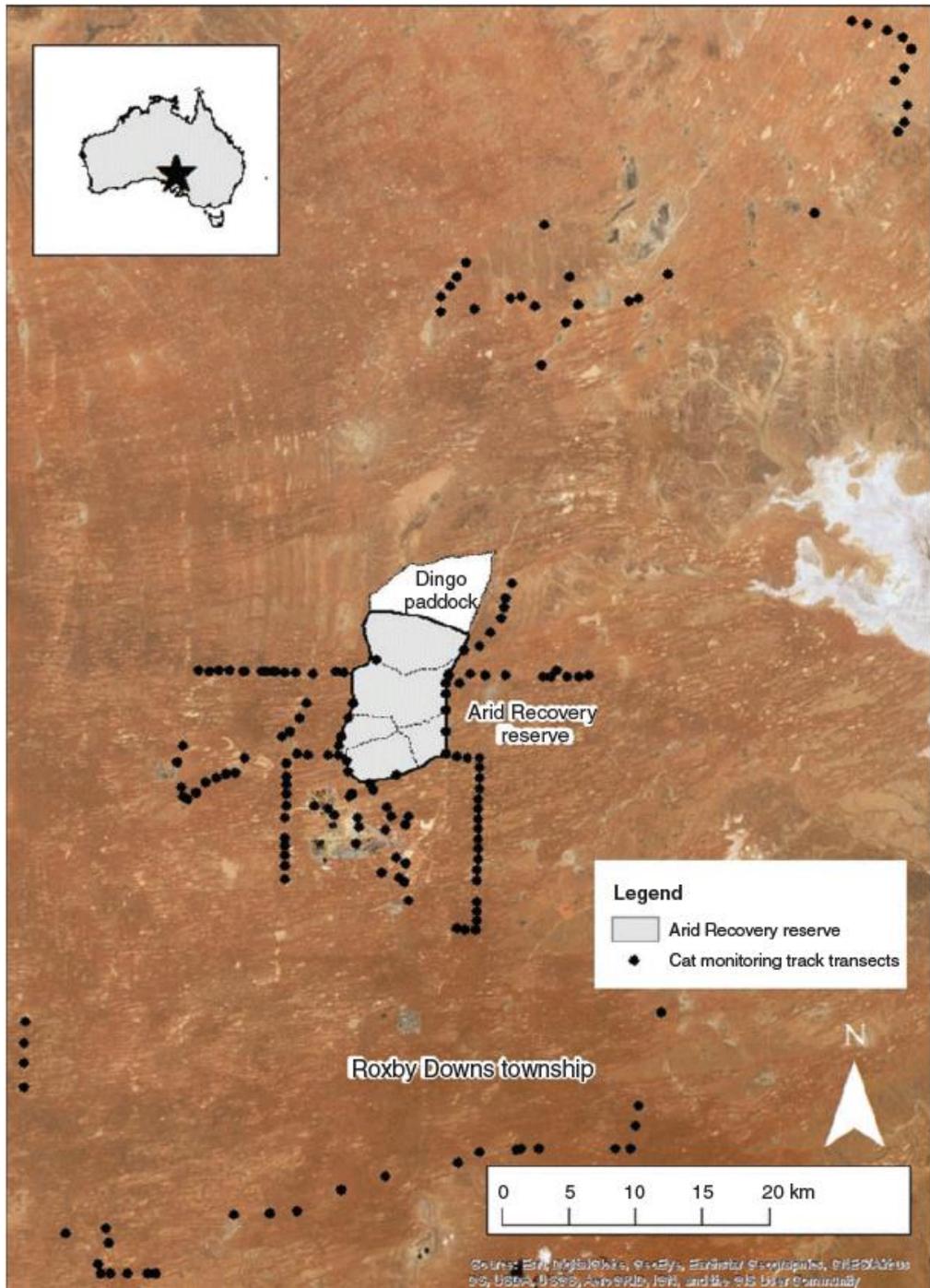


Figure 1: Map of the Arid Recovery reserve (grey) and the other fenced area (dingo paddock, white), including locations of all the cat-monitoring transects used in the analysis to investigate whether cats are likely to be found closer to the reserve, because small mammals inside the reserve increase in density, causing a corresponding increase outside the fence. Monitoring transects from ([Moseby and Hill 2011](#)).

Because each transect was sampled several times and only presence/absence of cats was analysed, we analysed data using mixed-effects generalised linear models with a binomial distribution, by using the 'lme4' library ([Bates et al. 2015](#)) in R ver. 3.6.1 ([R Core Team 2019](#)). We compared different variables in a model-averaging information-theory framework ([Barton 2011](#)). Variables included distance to Arid Recovery perimeter fence (also a version log-transformed, to account for a potential clumping-effect on the fence), an interaction with year (expressed as a continuous variable),

adjacent to any barrier fence (either the Arid Recovery fence, dog-fence, or town rabbit-proof fence), rainfall over the preceding 6 months (records from Olympic Dam Aerodrome, www.bom.gov.au/climate/data, accessed 12 October 2019, maximum nightly temperature, presence of dingo tracks also on transect, whether transect was north or south of the dog fence, number of cats removed from the area within the previous 6 months, and whether poison baiting was conducted in the previous 6 months at the transect. If cat activity increased near the reserve once native rodents became established and started spilling into the surrounding landscape, we would expect the interaction between the two variables of distance to fence and year to be of high importance in the models. The winning model was visually presented with the 'effects' library ([Fox and Weisberg 2019](#)).

Are native rodents more likely to be found in the stomachs of cats near the reserve edge?

To determine whether feral cats near the reserve fence are more likely to eat native rodents, we looked at stomach contents of cats killed as part of ongoing control operations and related these diet samples to a range of variables. We analysed diet samples of cats from 2012 to 2018, after the effects of major rainfall in 2010 had subsided. We also considered only cats caught within 50 km of the reserve, and those for which all data collection was complete. Cats were caught either in soft-jaw leg-traps around the reserve perimeter, or by shooting around the reserve and on the surrounding cattle stations (Stuart Creek, Andamooka Station and Roxby Station). For every cat killed, we recorded date, weight, pelage (tabby, ginger, black or misc), sex, stomach contents, location and distance from the reserve fence. The latter was either an exact GPS location, or an approximate distance from known landmark (e.g. '500 m west of Pine Dam'). We excluded cats that weighed less than 1.3 kg because they may have been unweaned, with their stomach contents not being representative of their hunting.

For analysis, our response variable was the count of spinifex hopping mouse and/or plains mouse in stomach contents. Explanatory variables were trapping method, cat weight, pelage, method of capture (shot or trapped) and distance to the reserve fence. Because the counts were zero-inflated, we used two-stage hurdle models, using the 'pscl' library in R. ver. 3.6.1.5, which essentially run a combination of a binomial model stage for the presence/absence, then a Poisson model stage only for the counts ([Kleiber and Zeileis 2016](#)). Model selection was conducted within an information-theory framework ([Burnham and Anderson 1998](#)). First, we compared the best way to consider distance to the Arid Recovery perimeter fence. We created five models to test different possible relationships of distance to the reserve to determine which was most parsimonious, including untransformed, transformed either by log, square-root, or squared, or a binary variable of transect being adjacent to the fence (<50 m). The best-performing distance variable was then used in a broader set of models, including all other variables in either the binomial or Poisson segment of the two-stage hurdle models. With this larger set of models, we used model averaging and created a winning model, including variables with >73% relative importance, suggesting an Akaike information criterion (AIC) difference of 2 or less ([Richards 2005](#)). Results were visually presented using the library 'ggplot2' ([Wickham 2016](#)).

Do individual cats selectively hunt near the reserve edge?

To determine whether cats selectively hunt at the reserve fences in a situation where there is no cat control, we used data from GPS-collared cats inside one of the Arid Recovery research fenced areas (the Dingo Paddock) in 2016 and 2017. This fenced area is 37 km², and is surrounded by a floppy-top fence ([Moseby and Read 2006](#); [Moseby et al. 2018](#)). The Dingo Paddock is roughly triangle-shaped, with only the southern side abutting the sections of the reserve with a high rodent density ([Fig. 2](#)).

This southern fence has an inward-facing floppy top, whereas the other fences have an outward-facing floppy top. Any cat within this fenced area would have a choice of hunting along this southern fence or the other fences.

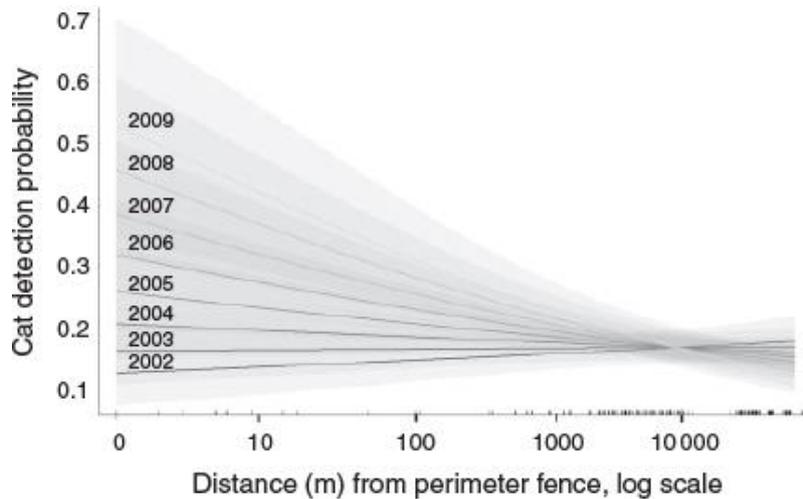


Figure 2: Model output of presence of cat tracks on track transects at different distances to the Arid Recovery fence (log-transformed) in successive years. Shaded bands represent 95% confidence intervals.

In 2016/17, we deployed GPS collars (Robin tags, Advanced Telemetry Systems Australia, Gold Coast, Qld, Australia) on 17 feral cats in the 37-km² fenced area. The cats were already living within this paddock. Each collar was programmed to obtain fine-scale movement data, and record positional fixes at 2.5-min intervals. A habitat layer was made using aerial photography to distinguish the key habitats, namely, dune, swale, claypan and creek line. We also created a buffer of 100 m along each fence line (southern, northern and western); only the southern fence line formed part of the boundary with the rest of the reserve. There were scattered water leaks in an underground pipeline along this southern boundary. To disentangle the effects of these, we mapped all permanent puddles created by these leaks and water sources (e.g. dams) and created a 200-m buffer around them to use as a habitat variable. To analyse whether cats selectively hunt on the southern fence (reserve edge) over the other fenced sides, we created a biased random-bridge kernel for each individual cat ([Benhamou 2011](#)). Because we did not want habitat-usage patterns to be biased by single nights where cats walked back and forth along a fence (anecdotal observation shows that this could be the case), we created a 95% utility distribution for each night, essentially a polygon of where it was 95% likely the cat visited that night. All nights were combined for each individual. As a result, repeated visits to the same area in one night counted only as a single visit each night. Using the Manly selective measure to test for significant differences in used versus available habitat in 'adehabitatHS' ([Calenge 2011](#)) in R ver. 3.6.1, we then compared the portion of used habitat to the habitat available in their whole home range, determined using the non-parametric local convex hull method ([Getz et al. 2007](#)). This library was also used to present results.

Results

Are feral cats more likely to be detected closer to the reserve edge over time as populations of native rodents gradually increase inside the reserve?

Between 2002 and 2009, animal tracks were sampled on 161 transects, with each transect being sampled, on average, 32 times for this analysis, with a total of 5172 occasions. We used this dataset to examine the relationship between the probability of detecting a cat on the transect and the distance to the Arid Recovery fence. The most important variables for explaining the presence of cat tracks on transects were year and an interaction between the log-transformed distance to the reserve and year; there was also strong support for occurrence of recent baiting, and maximum temperature (importance >0.73, Table 1). Cat tracks were significantly more likely to be detected closer to the Arid Recovery fence as years progressed (Fig. 2).

Table 1. Importance of different variables for explaining presence of cat tracks on track transects surrounding the Arid Recovery fence between 2002 and 2009
Significant values are shown in bold

Variable	Importance	Number of models	Coefficient	s.e.	z	P-value
Log(distance to reserve)	1.00	96	0.07	0.05	1.41	0.159
Year	0.99	96	0.30	0.09	3.34	0.001
Log(distance to reserve) × year	0.99	32	-0.03	0.01	3.17	0.002
After baiting	0.91	80	-0.19	0.10	1.97	0.049
Maximum temperature	0.81	80	0.42	0.30	1.41	0.159
Rainfall	0.34	80	-0.06	0.15	0.39	0.699
Dingo tracks	0.29	80	-0.02	0.08	0.21	0.831
Next to fence	0.28	80	-0.02	0.11	0.20	0.845

Are native rodents more likely to be found in the stomachs of cats near the reserve edge?

Between January 2012 and August 2018, 618 cats, in total, were shot or trapped around the reserve. From these, 585 were used in the analysis (i.e. weight >1.3 kg, <50 km from reserve, full stomach data collected). Of these, 388 were shot and 197 were trapped. Spinifex hopping mice or plains mice were found in 24% of cat stomachs, with there being, typically, several individuals in each stomach (average 2.2 rodents per stomach, maximum = 9). The most parsimonious variable for considering distance to the reserve and count of these rodents in stomachs was after square-root transformation (Akaike weight = 0.93, Table 2). Once distance to fence with this square-root relationship was considered against all other modelled variables in a model-averaging framework, it was found to be the most important variable, with cat weight and recent rainfall also demonstrating importance (Table 3). The output of this model suggests that cats collected adjacent to the reserve would have an average of one rodent in stomach contents, with this declining to 0.3 at a distance of 10 km (Fig. 3).

Table 2. Comparison of hurdle models of count of native rodents in cat stomachs, with five different transformations of distance to fence. Sqrt, square root

Parameter	d.f.	logLik	AICc	Delta	Weight
Sqrt(distance)	4	-484.7	977.4	0	0.93
Log(distance)	4	-487.3	982.6	5.3	0.07
Distance	4	-490.8	989.7	12.3	0
Distance ²	4	-496.4	1000.8	23.4	0
Next to fence?	4	-508.3	1024.7	47.3	0

Table 3. Importance of different variables for explaining counts of native rodents in cat stomachs using Akaike information criterion corrected for small sample sizes (AICc) model averaging based on two-stage hurdle models. ‘Zero’ variables refer to variables relating to the presence/absence of rodents, and ‘count’ variables relate to those affecting the number of individuals found in cat stomachs, once more than one is detected. Significant values are shown in bold

Variable	Description	Importance	Coefficient	s.e.	z	P-value
Zero	Sqrt(distance)	1.00	−0.02	0	4.63	<0.001
Zero	Rainfall	1.00	2.44	0.52	4.69	<0.001
Zero	Cat weight	0.95	−0.38	0.17	2.33	0.020
Count	Rainfall	0.64	0.59	0.60	0.98	0.326
Count	Sqrt(distance)	0.48	0	0	0.66	0.511
Zero	Trapped	0.45	−0.13	0.22	0.62	0.537
Count	Trapped	0.43	−0.13	0.22	0.58	0.563
Count	Cat weight	0.27	0.01	0.06	0.12	0.906
Zero	Pelage	0.21	0.04	0.52	0.08	0.938

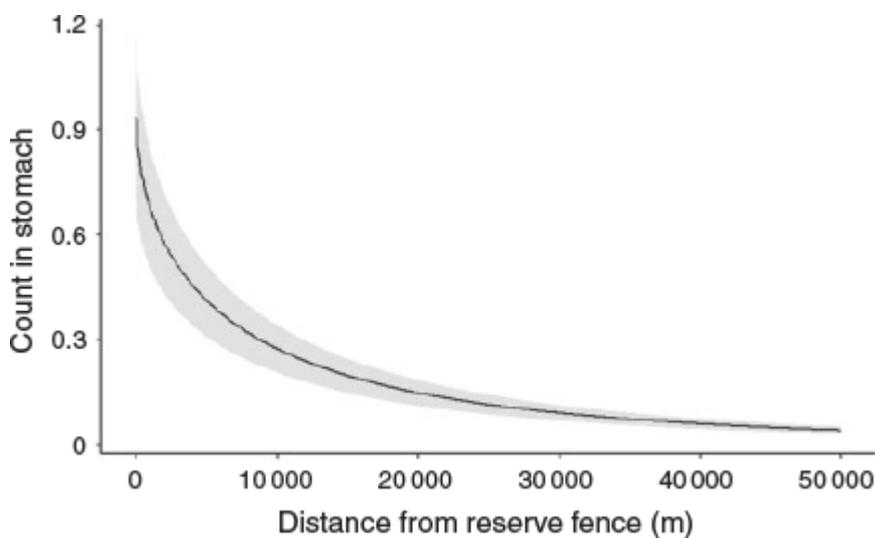


Figure 3: Model predictions of relationship between rodents in cat stomachs and distance to fence from the most parsimonious model determined by Akaike information criterion (AIC) model selection. Shaded bands represent 95% confidence intervals.

Do individual cats selectively hunt near the reserve edge?

Between June 2016 and May 2017, 17 feral cats were captured in a 37-km² fenced Dingo Paddock of Arid Recovery, where only the southern edge abuts the rest of the reserve. Of the 17 cats, we obtained fine-scale GPS data of more than 2 weeks from 10 individuals (average = 20 days, max = 29 days). On the basis of non-parametric local convex hull home-range estimates, home ranges were between 70 and 1130 ha (average = 472 ha, s.e. = 105 ha). After biased random bridges were used to assess habitat usage, preference for the southern boundary fence was found to have the highest Manly selectivity ratio (2.4, s.e. = 0.33, [Fig. 4](#)), and it was significantly different from the other habitat variables (Bonferroni, 95%). Water sources were also significantly selected for (Manly selectivity ratio = 1.6, s.e. = 0.21), whereas other variables were not ([Fig. 4](#)). The preference for the southern boundary varied among individual cats, with eight cats selecting for it (e.g. [Fig. 5a](#)), and two living away from the fence and never visiting it (e.g. [Fig. 5b](#)).

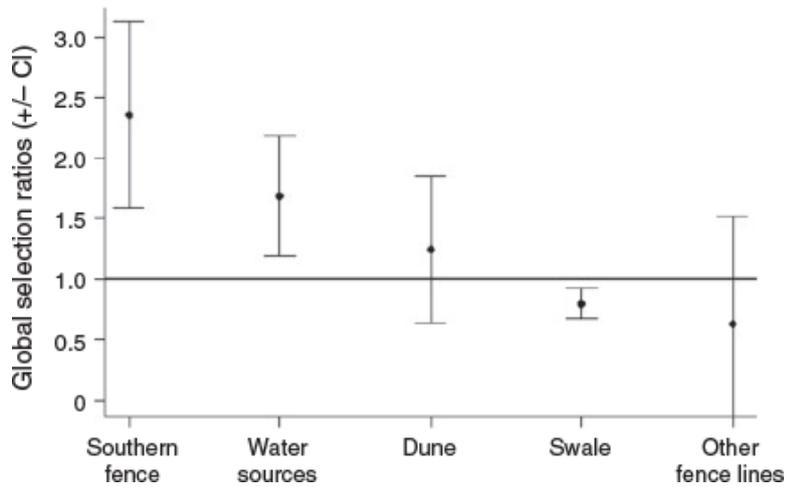


Fig. 4. Habitat selectivity of all 10 cats in a 37-km² fenced area at Arid Recovery. The southern fence is the only one connected to the rest of the reserve with abundant critical weight-range rodents.

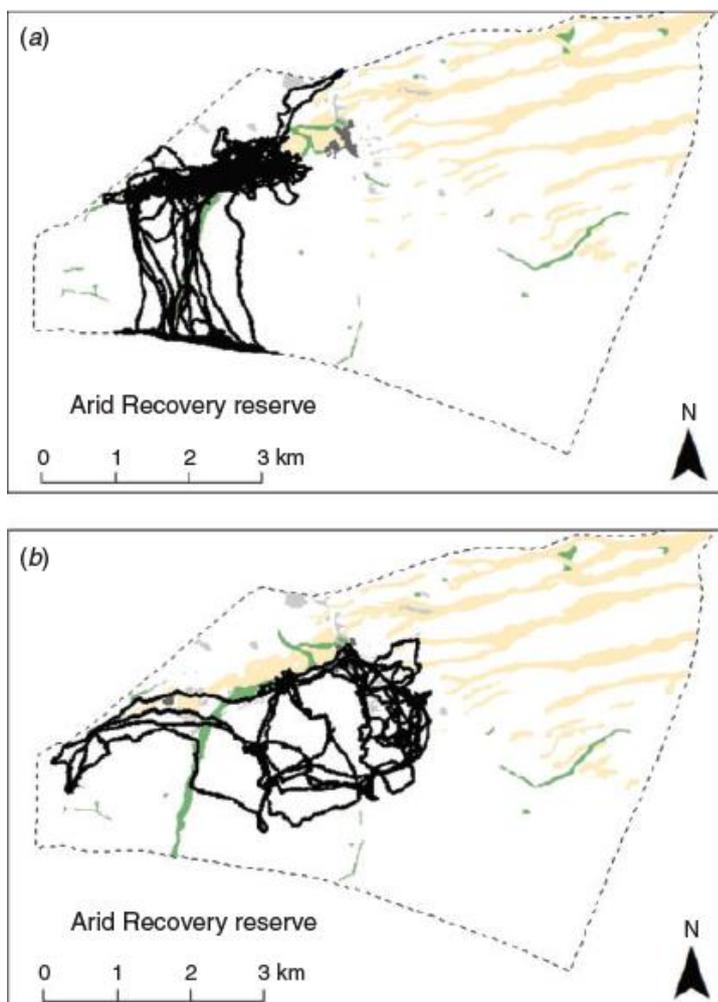


Fig. 5. Movements of 2 of the 10 feral cats within in a 37-km² fenced area at Arid Recovery (black lines), with a background of different vegetation types (white = swale, orange = dune, green = creek line) and perimeter fence (dashed line). These cats represent a range of interactions with the boundary fence next to the Arid Recovery reserve, from (a) considerable use (representing 8 of 10 cats) to (b) never visiting it representing 2 of the 10 cats).

Discussion

Successful conservation reserves may inadvertently attract cats to their edges and increase their abundance by creating a zone in which availability of a preferred food source (in this case, native rodents) is elevated. The predator-proof fence surrounding the Arid Recovery reserve has enabled many native species to thrive, including two native rodents that have been able to seed the surrounding landscape ([Moseby et al. 2019](#)). Cats appear to be aware of prey dispersing through the fence, and cat activity along the fence line increased in tandem with the increase in rodents within the reserve from 2002 to 2009. This corroborates the report of greater cat activity adjacent to the fence in a recent study ([Moseby et al. 2019](#)). Our results are unlikely to be due to a barrier effect caused by cats encountering and following fence lines, as neither the track counts nor GPS tracking uncovered any evidence for a general fence effect, only an attraction to fences protecting a dense population of native rodents that filtered through. Therefore, we conclude that there is now a greater pressure of cats on the edge of this fenced reserve than there was before spinifex hopping mice and plains mice re-established.

The small mammals dispersing through the fence would represent a substantial food source for feral cats. Each stomach from a cat collected near the perimeter fence had an average of one spinifex hopping mouse or plains mouse, and some cats had up to eight or nine. Each of these rodents weigh 30–70 g, and each would be likely to contain ~600–1400 kJ of energy ([Clum et al. 1996](#); [Plantinga et al. 2011](#)). Considering that the average required energy intake for a feral cat is ~1100 kJ per day ([Plantinga et al. 2011](#)) and each stomach content is likely to represent 8–12 h of hunting ([Chandler et al. 1997](#)), consuming just two rodents per day around the fence line would be extremely profitable for feral cats.

The higher activity of cats along the Arid Recovery fence is despite consistent feral-predator control. While cat-control effort has been variable, with some years having over 7000 soft-jaw leg-trap-nights and 100 shooting runs, and others considerably fewer, on average, 104 cats have been removed from within 1 km of the reserve edge every year from 2002 to 2018 (range 22–202 cats, Arid Recovery, unpubl. data). From 2012 to 2018, over 600 feral cats were removed from the vicinity of the fence. Yet, even this effort appears to have been unable to offset constant reinvasion of cats, as has been reported in other cat-control programs in open landscapes ([Lazenby et al. 2014](#)), nor has it allowed populations of other larger critical weight-range animals to flourish in the area ([Moseby et al. 2011, 2019](#)).

Our results reinforce the hypothesis that the exterior of fenced reserves is particularly attractive to predators. Cats travel large distances and are aware of areas of high prey availability, even if these are outside their home range ([Moseby et al. 2009b](#); [McGregor et al. 2016](#)). Once predators become aware of such available food sources, they would be likely to focus activity there and visit repeatedly. For example, [Frank et al. \(2014\)](#) found that once individual feral cats became aware of a population of long-haired rats, *Rattus villosissomus*, inside an experimental pen, they repeatedly returned until the native rat population was extirpated. Furthermore, if cats are more likely to visit the edges of fenced reserves, they would also presumably be more likely to take advantage of breaches or holes as they occur. Feral cat breaches in another conservation reserve (Currawinya) were soon followed by a rapid increase in cat signs over the following 2 years, and a subsequent local extinction of bilbies ([Lollback et al. 2015](#)). This highlights the importance of long-term fence maintenance and perimeter predator control for fenced conservation reserves.

This zone of elevated predator activity around predator-fenced reserves could represent a lethal barrier, preventing emigration and establishment of other species beyond reserve boundaries. This

problem would be especially acute in situations where reserves contain small and highly fecund animals that are able to increase to high numbers inside the fence, then disperse through the fence to create high prey availability immediately outside. The impacts of elevated cat activity close to reserve boundaries on other *in situ* fauna such as native reptiles and birds have not been studied; however, it is possible that species in the immediate vicinity of fenced reserves may be negatively affected.

The concentration of predator activity immediately outside reserve fences also offers an opportunity for strategic control. If such areas create a concentration of cats along a linear barrier, they would be ideal locations for trapping, shooting or deploying Felixer™ grooming traps (Read *et al.* 2019). Another potential tool to target elevated feral-predator numbers preying on small mammals emigrating from fenced reserves are micro-chip-sized lethal implants (Read *et al.* 2015) that could be inserted into small mammals that are likely to breach reserve fences, so as to control high densities of predators outside.

Our research suggests that feral cats are aware, and can take advantage of, local increases in prey availability, such as those that can occur immediately outside fenced conservation reserves. Managers of fenced conservation reserves should be mindful that increasing predator control around conservation reserves may be critical for offsetting elevated impacts on surrounding fauna from predators responding to spill-over effects of prey that can breach these fences (Moseby *et al.* 2019).

Acknowledgements

Arid Recovery is 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. Numerous volunteers and staff assisted with collecting track count data, including Nicki Munro, Jenny Stott, Jeff Turpin, Jason Briffa, Bree Galbraith, Michelle Thums and Adam Bester. Katherine Tuft and Zac Richardson assisted with field data collection of GPS-collared cats. Hugh McGregor and Sarah Legge are supported by the National Environmental Science Program's Threatened Species Recovery Hub. Ethics approval for the track counts was granted by the South Australian Wildlife Ethics Committee (Permits 14/2002 and 9/2006), and GPS collaring of cats was approved by University of Tasmania Animal Ethics Committee (A0015720).

References

- Barton, K. (2011). 'MuMIn: Multi-model Inference. R Package Version 1.0. 0.' (R Foundation for Statistical Computing: Vienna, Austria.) Available at <http://CRAN.R-project.org/package=MuMIn> [verified 8 May 2020].
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67, 1–48.
- Benhamou, S. (2011). Dynamic approach to space and habitat use based on biased random bridges. *PLoS One* 6, e14592.

Bodey, T. W., Bearhop, S., and McDonald, R. A. (2011). Localised control of an introduced predator: creating problems for the future? *Biological Invasions* 13, 2817–2828.

Burnham, K. P., and Anderson, D. R. (1998). 'Model Selection and Multimodel Inference: a Practical Information-theoretic Approach.' 2 edn. (Springer Science & Business Media, Inc: New York, NY, USA.)

Burns, B., Innes, J., and Day, T. (2012). The use and potential of pest-proof fencing for ecosystem restoration and fauna conservation in New Zealand. In 'Fencing for Conservation'. (Eds J. M. Somers, and M. Hayward.) pp. 65–90. (Springer: New York, NY, USA.)

Butler, K., Paton, D., and Moseby, K. (2019). One-way gates successfully facilitate the movement of burrowing bettongs (*Bettongia lesueur*) through exclusion fences around reserve. *Austral Ecology* 44, 199–208.

Calenge, C. (2011). 'Exploratory Analysis of the Habitat Selection by the Wildlife in R: the adehabitatHS Package.' (Office National de la Chasse et de la Faune Sauvage: Saint Benoist, France.)

Chandler, M. L., Guilford, G., and Lawoko, C. R. (1997). Radiopaque markers to evaluate gastric emptying and small intestinal transit time in healthy cats. *Journal of Veterinary Internal Medicine* 11, 361–364.

Clum, N. J., Fitzpatrick, M. P., and Dierenfeld, E. S. (1996). Effects of diet on nutritional content of whole vertebrate prey. *Zoo Biology* 15, 525–537.

Denny, E. A., and Dickman, C. R. (2010). 'Review of Cat Ecology and Management Strategies in Australia.' (Invasive Animals Cooperative Research Centre: Canberra, ACT, Australia.)

Fox, J. E. D., and Weisberg, S. (2019) 'An R Companion to Applied Regression.' 3rd edn. (Sage: Thousand Oaks, CA, USA.)

Frank, A. S. K., Johnson, C. N., Potts, J., Alaric, F., Lawes, M. J., Woinarski, J. C. Z., Tuft, K., Radford, I., Gordon, I. J., Collis, M.-A., and Legge, S. (2014). Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savanna. *Journal of Applied Ecology* 51, 1486–1493.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., and Wilmers, C. C. (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2, e207.

Hayward, M. W., and Somers, M. J. (2012). An introduction to fencing for conservation. In 'Fencing for Conservation'. (Eds M. J. Somers, and M. W. Hayward.) pp. 1–6. (Springer.)

Hayward, M. W., L'Hotellier, F., O'Connor, T., Ward-Fear, G., Cathcart, J., Cathcart, T., Sephens, J., Stephens, J., Herman, K., and Legge, S. (2012). Reintroduction of bridled nailtail wallabies beyond fences at Scotia Sanctuary – Phase 1. *Proceedings of the Linnean Society of New South Wales* 134, A27–A37.

Hayward, M. W., Poh, A. S. L., Cathcart, J., Churcher, C., Bentley, J., Herman, K., Kemp, L., Riessen, N., Scully, P., Diong, C. H., Legge, S., Carter, A., Gibb, H., and Friend, J. A. (2015). Numbat nirvana: conservation ecology of the endangered numbat (*Myrmecobius fasciatus*) (Marsupialia: Myrmecobiidae) reintroduced to Scotia and Yookamurra Sanctuaries, Australia. *Australian Journal of Zoology* 63, 258–269.

Holdaway, R. N. (1999). Introduced predators and avifaunal extinction in New Zealand. In 'Extinctions in Near Time'. (Ed. R. D. E. MacPhee.) pp. 189–238. (Springer: New York, NY, USA.)

Kanowski, J., Roshier, D., Smith, M., and Fleming, A. (2018). Effective conservation of critical weight range mammals: reintroduction projects of the Australian Wildlife Conservancy. In 'Recovering Australian Threatened Species: a Book of Hope'. (Eds S. Garnett, J. C. Z. Woinarski, D. Lindenmayer, and P. Latch.) p. 269. (CSIRO Publishing: Melbourne, Vic., Australia.)

Kleiber, C., and Zeileis, A. (2016). Visualizing count data regressions using Rootograms. *The American Statistician* 70, 296–303.

Lazenby, B. T., Mooney, N. J., and Dickman, C. R. (2014). Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. *Wildlife Research* 41, 407–420.

Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Radford, J. Q., Mitchell, N., Bode, M., Wintle, B., Baseler, M., Bentley, J., Copley, P., Dexter, N., Dickman, C. R., Gillespie, G. R., Hill, B., Johnson, C. N., Latch, P., Letnic, M., Manning, A., McCreless, E. E., Menkhorst, P., Morris, K., Moseby, K., Page, M., Pannell, D., and Tuft, K. (2018). Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research* 45, 627–644.

Loarie, S. R., Van Aarde, R. J., and Pimm, S. L. (2009). Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation* 142, 3086–3098.

Lollback, G. W., Mebberson, R., Evans, N., Shuker, J. D., and Hero, J. (2015). Estimating the abundance of the bilby (*Macrotis lagotis*): a vulnerable, uncommon, nocturnal marsupial. *Australian Mammalogy* 37, 75–85.

- McGregor, H. W., Legge, S., Jones, M. H., and Johnson, C. N. (2016). Extraterritorial hunting expeditions to intense fire scars by feral cats. *Scientific Reports* 6, 22559.
- Miskelly, C. M., and Powlesland, R. G. (2013). Conservation translocations of New Zealand birds, 1863–2012. *Notornis* 60, 3–28.
- Moseby, K. E., and Hill, B. M. (2011). The use of poison baits to control feral cats and red foxes in arid South Australia I. Aerial baiting trials. *Wildlife Research* 38, 338–349.
- Moseby, K. E., and Read, J. L. (2006). The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. *Biological Conservation* 127, 429–437.
- Moseby, K. E., Hill, B. M., and Read, J. L. (2009a). Arid Recovery: a comparison of reptile and small mammal populations inside and outside a large rabbit, cat and fox-proof enclosure in arid South Australia. *Austral Ecology* 34, 156–169.
- Moseby, K. E., Stott, J., and Crisp, H. (2009b). Movement patterns of feral predators in an arid environment: implications for control through poison baiting. *Wildlife Research* 36, 422–435.
- Moseby, K. E., Read, J. L., Paton, D. C., Copley, P., Hill, B. M., and Crisp, H. A. (2011). Predation determines the outcome of 10 reintroduction attempts in arid South Australia. *Biological Conservation* 144, 2863–2872.
- Moseby, K. E., Neilly, H., Read, J. L., and Crisp, H. A. (2012). Interactions between a top order predator and exotic mesopredators in the Australian rangelands. *International Journal of Ecology* 2012, 1–15.
- Moseby, K., Crowther, M., and Letnic, M. (2018). Ecological role of an apex predator revealed by a reintroduction experiment and Bayesian statistics. *Ecosystems* 34, 283–295.
- Moseby, K., McGregor, H., Hill, B. M., and Read, J. (2019). Exploring the internal and external wildlife gradients created by conservation fences. *Conservation Biology* 34, 220–231.
- Pedler, R. D., Brandle, R., Read, J. L., Southgate, R., Bird, P., and Moseby, K. E. (2016). Rabbit biocontrol and landscape-scale recovery of threatened desert mammals. *Conservation Biology* 30, 774–782.
- Plantinga, E. A., Bosch, G., and Hendriks, W. H. (2011). Estimation of the dietary nutrient profile of free-roaming feral cats: possible implications for nutrition of domestic cats. *British Journal of Nutrition* 106, S35–S48.

R Core Team (2019). R: a language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna, Austria.) Available at <https://www.R-project.org/> [verified 8 May 2020].

Read, J. L., and Cunningham, R. B. (2010). Relative impacts of cattle grazing and feral animals on an Australian arid zone reptile and small mammal assemblage. *Austral Ecology* 35, 314–324.

Read, J. L., and Eldridge, S. (2010). An optimised rapid detection technique for simultaneously monitoring activity of rabbits, cats, foxes and dingoes in the rangelands. *The Rangeland Journal* 32, 389–394.

Read, J. L., Peacock, D., Wayne, A. F., and Moseby, K. E. (2015). Toxic Trojans: can feral cat predation be mitigated by making their prey poisonous? *Wildlife Research* 42, 689–696.

Read, J., Copley, P., Ward, M., Dagg, E., Olds, L., Taggart, D., and West, R. (2018). Bringing back waru: return of the black-footed rock-wallaby to the APY Lands. In 'Recovering Australia's Threatened Species: a Book of Hope'. (Eds S. Garnett, P. Latch, D. Lindenmayer, and J. Woinarski.) pp. 237–248. (CSIRO: Melbourne, Vic., Australia.)

Read, J. L., Bowden, T., Hodgens, P., Hess, M., McGregor, H., and Moseby, K. (2019). Target specificity of the felixer grooming 'trap'. *Wildlife Society Bulletin* 43, 112–120.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86, 2805–2814.

Russ, G. R., and Alcala, A. C. (2011). Enhanced biodiversity beyond marine reserve boundaries: the cup spillith over. *Ecological Applications* 21, 241–250.

Saunders, A., and Norton, D. (2001). Ecological restoration at mainland islands in New Zealand. *Biological Conservation* 99, 109–119.

Tanentzap, A. J., and Lloyd, K. M. (2017). Fencing in nature? Predator exclusion restores habitat for native fauna and leads biodiversity to spill over into the wider landscape. *Biological Conservation* 214, 119–126.

Wickham, H. (2016) 'ggplot2: Elegant Graphics for Data Analysis.' (Springer-Verlag: New York, NY, USA.)

Woinarski, J. C. Z., Burbidge, A. A., and Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America* 112, 4531–4540.

Woolley, L.-A., Geyle, H. M., Murphy, B. P., Legge, S. M., Palmer, R., Dickman, C. R., Augusteyn, J., Comer, S., Doherty, T. S., Eager, C., Edwards, G., Harley, D. K. P., Leiper, I., McDonald, P. J., McGregor, H. W., Moseby, K. E., Myers, C., Read, J. L., Riley, J., Stokeld, D., Turpin, J. M., and Woinarski, J. C. Z. (2019). Introduced cats *Felis catus* eating a continental fauna: inventory and traits of Australian mammal species killed. *Mammal Review* 49, 354–368.