

Direct evidence implicates feral cat predation as the primary cause of failure of a mammal reintroduction programme

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Mike Calver is an Associate Professor in Animal Ecology at the School of Veterinary Life Sciences Murdoch University (Environment and Conservation Cluster) (Murdoch, Western Australia 6150, Australia; Email: m.calver@murdoch.edu.au). This project, re-establishing two species of bare-wallaby onto Peron Peninsula, arose from other projects within the arm of Project Eden, managed by the Department of Conservation and Environment, which aimed to reintroduce locally extinct mammal fauna to their former range.

Summary As evidence mounts that the feral Cat (*Felis catus*) is a significant threat to endemic Australian biodiversity and impedes reintroduction attempts, uncertainty remains about the impact a residual population of cats following control will have on a mammal reintroduction programme. Also, behavioural interactions between cats and their prey continue to be an area of interest. Within the framework of an ecosystem restoration project, we tested the hypotheses that successful reintroductions of some medium-sized mammals are possible in locations where feral cats are controlled (but not eradicated) in the absence of European Red Fox (*Vulpes vulpes*), and that hare-wallabies that dispersed from their release area are more vulnerable to cat predation compared with those that remain at the release site. We used radiotelemetry to monitor the survivorship and dispersal of 16 Rufous Hare-wallabies (*Lagorchestes hirsutus* spp.) and 18 Banded Hare-wallabies (*Lagostrophus fasciatus fasciatus*) reintroduced to four sites within Shark Bay, Western Australia. Nearly all foxes were removed and feral cats were subject to ongoing control that kept their indices low relative to prerelease levels. All monitored hare-wallabies were killed by cats within eight and 10 months following release. Significant predation by feral cats was not immediate: most kills occurred in clusters, with periods of several months where no mortalities occurred. Once a hare-wallaby was killed, however, predation continued until each population was eliminated. Animals remaining near their release site survived longer than those that dispersed. The aetiology of predation events observed offers new insights into patterns of feral cat behaviour and mammal releases. We propose a hypothesis that these intense per capita predation events may reflect a targeted hunting behaviour in individual feral cats. Even where feral cats are controlled, the outcome from consistent predation events will result in reintroduction failures. Managers considering the reintroduction of medium-sized mammals in the presence of feral cats should, irrespective of concurrent cat control, consider the low probability of success. We advocate alternative approaches to cat-baiting alone for the recovery of cat-vulnerable mammals such as hare-wallabies.

Key words: feral cat, invasive species, marsupial, predation, reintroduction.

Introduction

Since European settlement in 1788, over 10% of endemic terrestrial Australian mammals have become extinct (Woinarski *et al.* 2015). The exotic predators the European Red Fox (*Vulpes vulpes*) and feral Cat (*Felis catus*) are proposed as significant factors in the extinctions. There is conclusive experimental evidence implicating the fox (Kinnear 2002), but until recently the case against cats was contentious.

Despite data on the diets of feral cats (Doherty *et al.* 2015), evidence of their impact on prey populations was initially anecdotal (e.g. Horsup & Evans 1993), or inferred from failed reintroductions (e.g. Moseby *et al.* 2011a) or biogeographic patterns in mammal declines (Burbidge &

McKenzie 1989). This century, growing direct evidence including controlled experimentation confirmed that feral cats are a primary cause of local population decline in Australian fauna (e.g. Risbey *et al.* 2000; Frank *et al.* 2014). Woinarski *et al.* (2014, p. 869) concluded that ‘... across threatened and near threatened taxa, the most significant threats are predation by feral cats, inappropriate fire regimes, predation by red foxes and habitat loss and fragmentation’. Nevertheless, McGregor *et al.* (2015a) argued that quantifying the impacts of feral cats remains largely inferential due to their cryptic nature. Information on the extent of their impact remains critical to management.

Management options for feral cats in Australia are diverse. Exclusion fencing

has limited applications (Moseby & Read 2006; Robley *et al.* 2007; De Tores & Marlow 2012), as do trapping and shooting (Short *et al.* 2002; Fisher *et al.* 2014). Baiting is attractive over larger areas (Moseby *et al.* 2011b; Fisher *et al.* 2014), with some significant successes claimed (e.g. Algar *et al.* 2013). However, it may not be effective at low cat population densities (McGregor *et al.* 2015a) or when prey densities are high (Risbey *et al.* 1997). Given evidence that habitat structure can influence cats’ hunting success with cats preferring open areas (McGregor *et al.* 2015b) and mammals from such habitats at greater risk of decline (Lawes *et al.* 2015), landscape management for fire and large herbivore grazing may mitigate predation indirectly (McGregor *et al.*

2014). Detailed understanding of the ecology of feral cats in relation to environmental variability may facilitate such approaches (Bengsen *et al.* 2016).

Foxes are easier to control than feral cats because they take baits more readily (contrast Kinnear *et al.* 1988 with Doherty & Algar 2015), but targeting one exotic predator may cause mesopredator release in a manner similar to interactions between dingoes and feral cats (Glen & Dickman 2005; Brook *et al.* 2012; Kennedy *et al.* 2012). This relationship suggests that the removal of foxes may directly lead to an increase in feral cat populations. Species with low population densities or preference for open country are particularly vulnerable to predation by feral cats (Smith & Quin 1996; Lawes *et al.* 2015), which is an obstacle to reintroducing mammal fauna to parts of their historic range.

In this study, and within a larger ecological restoration project on Peron Peninsula (Western Australia), we investigated whether self-sustaining populations of the Rufous Hare-wallaby (RHW) (*Lagorchestes birsutus*, the central Australian subspecies called Mala) and the Banded Hare-wallaby (BHW) (*Lagostrophus fasciatus fasciatus*) could be re-established where foxes were largely eliminated (Morris *et al.* 2004) and feral cats were baited intensively (Algar & Burrows 2004). We tested the hypothesis that reintroductions of these medium-sized mammals were possible where populations of feral cats were actively controlled in the absence of foxes. We also tested the hypothesis that hare-wallabies dispersing from their release area are more vulnerable to cat predation because they may not be as familiar with their new environment (e.g. spending more time to find suitable food, refugia, etc.) compared with those remaining in proximity to the release site and who have established a stable home range (Hardman & Moro 2006a).

Methods

Location of experimental release sites

This study utilised a reintroduction programme for hare-wallabies and intensive

fox and cat control by the Western Australian Department of Conservation and Land Management (now the Department of Parks and Wildlife (DPaW)). The study was situated within the semi-arid Francois Peron National Park on the Peron Peninsula (Western Australia) and in the Shark Bay World Heritage Property (25° 44' S, 113° 32' E; Fig. 1). Our research was conducted during 2001 and 2002 within the context of a DPaW programme encompassing 1050 km² of Peron Peninsula, and aimed at reversing declines in several native species by controlling introduced feral predators and competitors and reintroducing native fauna from a captive breeding programme. Further descriptions of the study area are given in Hardman and Moro (2006a) and Beller (2014).

Foxes were eliminated through aerial and ground baiting (Morris *et al.* 2004). An electrified barrier fence across the narrow isthmus of the peninsula inhibited their return. Exotic Goat (*Capra hircus*) was also controlled, and Sheep (*Ovis aries*) eliminated. Track count indices of Rabbit (*Oryctolagus cuniculus*) over 8 years following the initial fox control operation indicated substantial seasonal fluctuations (Morris *et al.* 2004).

Background to feral cat control during reintroductions

Since April 1996, cats were actively controlled on Peron Peninsula by daily trapping and baiting resulting in approximately 75% of radio-collared cats killed relative to pre-baiting estimates. Initial cat control focused

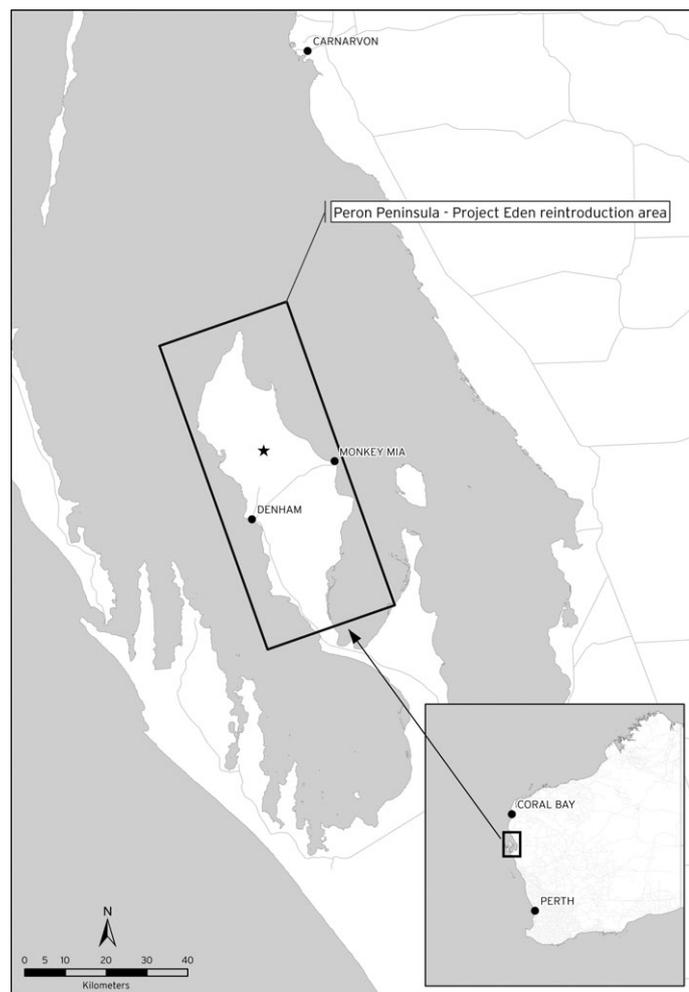


Figure 1. Schematic map illustrating the location of Peron Peninsula and the hare-wallaby release site (star symbol) within the Shark Bay World Heritage Area, Western Australia.

on using small, fresh meat 1080 baits coated in 'digest' dropped from an aircraft at 10 baits per square kilometre. Subsequent aerial and ground baiting in 2000 and 2001 used a cat sausage bait, resulting in some 80% of radio-collared cats killed relative to prebaiting estimates. A more detailed description of the cat-baiting strategy used is provided in Morris *et al.* (2004). Relative cat abundance (indirectly assessed as activity via track count indices) was estimated to be lower when hare-wallabies were released during August/September 2001 than earlier (Morris *et al.* 2004). Once hare-wallabies were released, no broad-scale leghold trapping (using 'Pongo' baits as lures) occurred for cats near the release sites to minimise the risk of hare-wallaby by catch.

Further cat control using aerial baiting occurred during autumn 2002 (7 months after releasing hare-wallabies; Algar & Burrows 2004). Postbaiting cat activity indices were estimated to be approximately 65% lower than prebaiting indices (Christensen *et al.* 2013), suggesting cat densities were likely lower during 2002 than previously (Morris *et al.* 2004).

Tracking hare-wallabies following release

Rufous Hare-wallaby (RHW; central Australian subspecies) males weigh from 0.8 to 1.6 kg, slightly heavier than females (0.9–1.3 kg) (Johnson & Burbidge 1998). Their distribution and behaviour are described in Langford and Burbidge (2001) and Hardman and Moro (2006a). Banded Hare-wallabies (BHW) weigh up to 2.1 kg (Prince 1998). Their distribution and behaviour are described in Short and Turner (1992), Helgen and Flannery (2003) and Hardman and Moro

(2006a). The released animals were bred in captivity within small predator-proof enclosures (approximately 0.1 ha) on the peninsula (Mawson 2004). Breeding stock of BHW was sourced from Bernier Island, and RHW, from a captive population in central Australia. The reintroduction occurred during August/September 2001 following winter rainfall. A total of 34 hare-wallabies were released – 16 RHW and 18 BHW – each carrying mortality-sensing radio transmitters. The animals, were released (Table 1) at four sites (each at least 1.5 km apart) (Hardman & Moro 2006b). Individuals were tracked on foot, or by airplane if a signal could no longer be obtained. Those that consistently chose diurnal refugia within 1 km of the release site were classed as residents, because no animal that moved more than 1 km during the study period returned to the release site (Hardman & Moro 2006b). Survivorship and distance travelled by each individual were determined daily for 2 weeks, then on alternate days thereafter.

Determining cause of death

We assessed individuals as dead when a carcass, or part thereof, was recovered, or a collar emitted a mortality signal in the same location more than once, when searching by airplane. Where an unattached collar was found, we assumed an individual had been decapitated because collars were of a smaller circumference than the head.

We identified cause of death from the forensic signature left by the predator when its tracks could be traced to a recent mortality site. Cat predation was recognised by fresh cat prints, and removal of flesh from skin and large bones (Short & Turner 2000). Predation by raptors was

identified by fresh raptor prints, raptor feathers and/or faeces, and the skin remaining at the feeding site. Cause of death was classified as 'indeterminate' if a carcass was recovered without signs of predation, and 'collar' where a dead animal had a limb entangled in the collar. Where possible, carcasses classified as 'indeterminate' were removed for postmortem examination. Animals whose collar signal was not located at the conclusion of the study were classified 'fate unknown'.

Data analysis

Data were observational, so survivorship and cause of death were described without statistical analysis. Pearson's correlation coefficient was used to assess correlations between the body weight of hare-wallabies prior to predation and their survival time, to determine whether hare-wallabies of a particular weight class were killed sooner by cats. Values are reported as mean \pm SD. Independent-sample *t*-tests were used to compare survivorship (days alive in the wild prior to death) between resident (<1 km) and emigrant (>1 km) individuals of each species.

To test whether hare-wallaby deaths were randomly distributed over time or aggregated, we counted the number of deaths in successive 5-day intervals from release for all four populations. We calculated the coefficient of dispersion (CD, variance/mean) as an indication of random (CD of approximately 1) or clumped (CD > 1) deaths, and also compared the data to a Poisson (random) distribution using chi-square goodness-of-fit tests.

Results

Survivorship of BHW following release

Once released, 11 of 18 (61%) BHW remained resident within 1 km of their release site. Residents survived for 103 days before the first death. At Site 1 all five resident individuals (15% of the entire released population) at were killed over 43 days from 104 to 147 days post-release (mean time between kills = 10.8 \pm 9.2 days). Three of the five BHW were killed within 6 days (Fig. 2a).

Table 1. Number and age of individual hare-wallabies released onto Peron Peninsula

Species	Site	Male	Female	Total	Dates of release	Mean age (month \pm SE)
Banded Hare-wallaby	1	6	3	9	06/08/01	16.2 \pm 1.7
	2	6	3	9	07/08/01	22.8 \pm 2.2
Rufous Hare-wallaby	3	3	3	6	03/09/01	13.3 \pm 1.9
	4	6	4	10	04/09/01	14.5 \pm 1.8
Total		21	13	34		

Site details refer to soft-released individuals (sites 1 and 3) or hard-released individuals (sites 2 and 4).

Similarly at Site 2 all six BHW individuals (18% of the released population) were killed within 28 days from 266 to 294 days postrelease (mean time between kills = 5.6 ± 6.8 days), and three of them within 2 days (Fig. 2b). Those killed on the same night were within 150 m of each other. No resident BHW survived more than 294 days.

Banded Hare-wallabies that emigrated 4.3–28 km from their release site ($n = 7$) fared similarly (Table 2). The average time

BHW survived away from the release site (mean = 39.5 ± 11.8 days postrelease) was significantly less than for those remaining at the release site (mean = 212 ± 23.3 days) ($t = 6.6$, d.f. = 13, $P < 0.01$).

Survivorship of RHW following release

Ten of 16 RHW remained resident. Residents survived for 2 days before the first death. RHW deaths also occurred over

two time periods. At Site 3 all four individuals were killed between 49 and 101 days postrelease (mean time between kills = 17.3 ± 3.2 days; Fig. 2c). At Site 4, three RHW were killed within three consecutive days 119 days postrelease (mean time between kills = 9.7 ± 4.2 days; Fig. 2d), and all within 150 m of each other. No resident RHW survived longer than 249 days (ca. 8 months) following release. In total for both species, there were four separate occasions where animals were killed on consecutive nights (Fig. 2).

RHW that emigrated from the release site ($n = 5$ or 83%) died. The average time RHW survived away from the release site (mean = 34.2 ± 9.4 days postrelease) was significantly lower than residents (mean = 103.4 ± 18.1 days) ($t = 3.4$, d.f. = 13, $P < 0.01$).

Cause of hare-wallaby deaths

All resident BHW and most RHW (70%) were killed by feral cats (Table 3). Two resident RHW were killed by raptors, probably Wedge-tailed Eagles (*Aquila audax*).

Over one-third (38%) of the hare-wallabies that emigrated from the release site were killed by feral cats (Table 2). Most emigrants with an unknown fate ($n = 4$) probably suffered the same demise.

The cause of death could not be determined for two RHW and one BHW. The carcasses were partly desiccated, there was no evidence of predator tracks, and postmortems remained inconclusive. However, none of these animals was thought to have suffered from predation (the bodies were generally intact) or from limb entanglement in collars.

In an attempt to prevent further cat-related deaths at Site 2, three poisoned sausage baits identical to those used for aerial baiting were placed in a BHW carcass the day after death. Next day the remains of the carcass were eaten, but not the baits.

The weight of BHW ($r_{14} = -0.17$, $P = 0.57$) or RHW ($r_9 = 0.21$, $P = 0.60$) had no effect on their ability to avoid predation, nor were hare-wallaby predation rates biased to any season.

Two RHW (one resident and one emigrant) probably died from collar-related

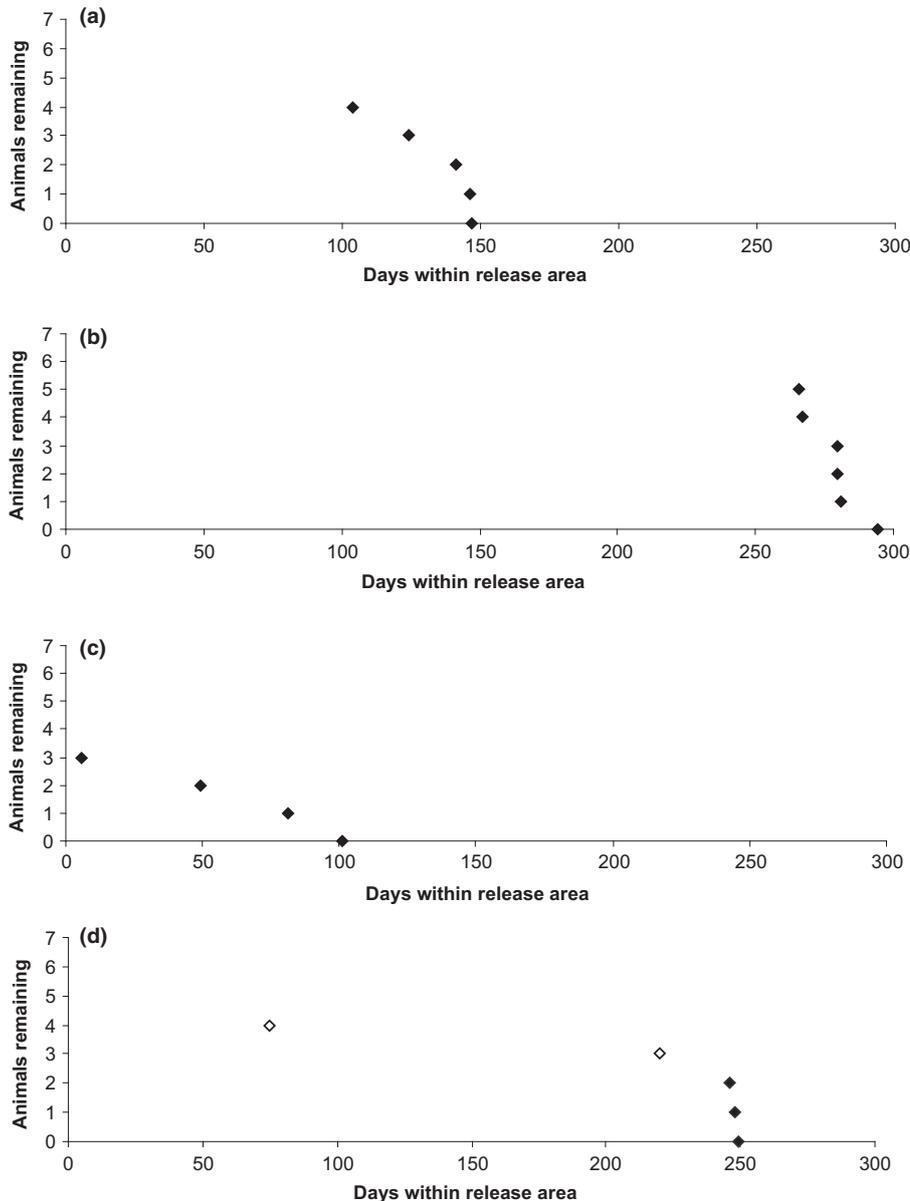


Figure 2. Number of days that Banded Hare-wallabies at Site 1 (a) and Site 2 (b), and Rufous Hare-wallabies at Site 3 (c) and Site 4 (d) persisted near their release site (<1 km of release) on Peron Peninsula before being killed. Mortalities reflect feral cat predation (closed diamonds) or avian predation (open diamonds) at each release site.

Table 2. Cause of mortality of hare-wallabies following release on Peron Peninsula, 2001–2002

Fidelity	Species	n (M, F)	cat	Raptor	Collar	Indeterminate	Fate unknown
Residents	Banded Hare-wallaby	11 (5, 6)	11	0	0	0	0
	Rufous Hare-wallaby	10 (4, 6)	7	2	1	0	0
Emigrants	Banded Hare-wallaby	7 (7, 0)	3	0	0	1	3
	Rufous Hare-wallaby	6 (5, 1)	2	0	1	2	1
Total		34 (21, 13)	23	2	2	3	4

Residents refer to those individuals that remained within 1 km of their release site. Emigrants refer to individuals that dispersed beyond 1 km from their release site.

Table 3. Details of Rufous Hare-wallaby ($n = 9$) and Banded Hare-wallaby ($n = 14$) carcasses following feral cat predation on Peron Peninsula, 2001–2002

Kill diagnostics	Rufous Hare-wallaby	Banded Hare-wallaby
Teeth marks present on collar	78	93
Decapitated	100	93
Brain eaten	14	22
Organs eaten	100	86
Stomach removed	88	86
Stomach buried	67	69
Body cached	29	25
Forelimbs present	38	21
Carcass drag length (m)†	22.4 (± 6.4)	11.3 (± 4.0)

Values are represented as percentages unless otherwise stated. †Mean \pm SE.

causes. Weight loss immediately after collaring is a known risk (e.g. Cypher 1997), as well as for pet cats that are lost and lose weight (Calver *et al.* 2013).

Description of cat predation

On no occasion did hare-wallaby or cat tracks in the sand provide evidence of a struggle or chase. The open nature of the habitat, together with early morning tracking before wind picked up, allowed observations of cat prints in the sand that led directly to a carcass.

Typical cat kills showed decapitation and stomach evisceration (Table 3). Thirteen carcasses (from 34 animals released) were located the day after death. Four were fully eaten (excluding stomach), seven were partially eaten and two remained whole (teeth puncture marks in the neck, tracks and drag marks confirmed death by cat predation). Thirteen of the 19 carcasses assessed were dragged for <20 m from the kill site; four 21–50 m, and two greater than 50 m. Of the carcasses not fully eaten ($n = 9$), four (two BHW, two RHW) were cached (partially buried). There was no evidence of fox activity from prints. Only cat prints were found. Four of the uneaten or partially

eaten carcasses were collected for post-mortems. Feral cat(s) returned to consume all remaining carcasses ($n = 5$).

Four females (3 BHW, 1 RHW) were killed whilst carrying pouch young 30–120 mm in length. When located, all joeys were dead, but showed no external injuries.

Patterns of hare-wallaby deaths

The combined data from all populations had a CD of 1.44, consistent with clumping, although the data were not significantly different from a Poisson distribution ($P > 0.05$).

Discussion

Despite ongoing cat control to keep their relative abundances below prerelease levels (Morris *et al.* 2004), feral cats killed at least 68% of released hare-wallabies within 10 months of release. Future releases of these medium-sized macropods are likely to suffer the same fate if reintroduced into areas with cat track indices of 15–64 (based on reported estimates of track count data from Christensen *et al.* 2013). This raises an ethical dilemma:

Should future releases of similar macropods into areas where feral cats occur – even when controlled – be supported by ethics committees? We suggest that researchers should justify why they believe the cat problem has been mitigated prior to future releases of similar species (e.g. training of released animals to recognise and avoid predators, or evidence of total predator removal). Although few animals were released, a larger founder number of hare-wallabies would have been no more likely to persist given the predation observed by feral cats elsewhere (Priddel & Wheeler 2004; Morris *et al.* 2004; Short *et al.* 1992). Thus, land managers should focus their efforts on feral cat control rather than increasing founding numbers.

Predators maximise their foraging efficiency by selecting prey with poor antipredator behaviour (Quinn & Cresswell 2004), so the vulnerability of prey to predators is important in their survivorship. Based on the observed forensics of each kill, there was no apparent attempt at evasion when cats killed hare-wallabies, supporting previous observations that hare-wallabies do not recognise cats as predators or lack suitable predator evasion skills (McLean *et al.* 1996; Short *et al.* 2002).

Elsewhere in Australia, feral cats coexist with some medium-sized mammals (Abbott 2002; Morris *et al.* 2004). The abundance of native mammals reintroduced into parts of south-western Australia initially increased over several years where foxes were controlled and where feral cats persisted (Mawson 2004), although some species later declined (Groom 2010). On islands off Western Australia, feral cats live alongside Tamar Wallaby (*Macropus eugenii*) and Quokka (*Setonix brachyurus*) (Short 1999).

Understanding the context of feral cat behaviour may address this paradox.

Little evidence of surplus killing by feral cats is known from Australia (McGregor *et al.* 2015b), although it occurs elsewhere (Peck *et al.* 2008; Stahl *et al.* 2001). The predation events observed at Peron did not reflect surplus kills because of feeding on at least some part of each carcass, and direct evidence that a predator returned to consume some of the (cached) carcasses.

Instead of surplus killing, we propose that individuals (e.g. male cats, see Moseby *et al.* 2015) 'prey-switched' (Murdoch & Oaten 1975), discovering and then actively targeting a new prey type abundant within a concentrated area. The hare-wallabies had been reintroduced within the cats' range and the cat(s) may have taken some time to become familiar with their new prey. After achieving a first kill they selectively hunted further hare-wallabies. Prey concentrated within an area persisted for some time before targeted predation began. Our suggestion of specific (rogue) cats being disproportionately responsible for the deaths of many reintroduced hare-wallabies is consistent with Moseby *et al.* (2015) who, based on a literature review and experimental analysis of the fate of reintroduced Western Quoll (*Dasyurus geoffroyii*), concluded that mature male cats exceeding 3.5 kg were more likely to kill larger, more challenging prey and potentially have the greatest impact on translocation success. They and others (see Read *et al.* 2015) advocate selective removal of these animals.

Other mammal recovery projects report significant mortality events prior to removing a specific predator. Gibson *et al.* (1994) found that predation of released RHW over 4 weeks ceased after a single large (5.1 kg) feral cat was trapped, despite other feral cats persisting. A single cat was also significant in the mortality of 57 adult allied Rock-wallaby (*Petrogale assimilis*) (Spencer 1990). Feral cats range up to 20 km per night in semi-arid environments (Edwards *et al.* 2001). In our study one or more feral cats may have achieved a first kill by chance and started targeting hare-wallabies. Without an experimental test

our explanation remains a hypothesis. However, we identify a pattern indicative of the clumping of deaths in time. Due to inadequate statistical power related to low sample size, this trend remains statistically insignificant. Future meta-analyses with more samples may clarify the patterns of mortalities observed.

Implications for managers

Feral cats, even when numbers were reduced by management actions, continue to threaten reintroductions. Whilst evidence for prey-switching as a potential contributor to the demise of the reintroduced population remains circumstantial, it is worth further investigation. We have no direct data on individual cat behaviours. The pattern of clumped deaths observed following general reductions in the feral cat population is in common to similar patterns observed elsewhere, suggesting that targeting specific problem cats may be effective in increasing translocation success (Moseby *et al.* 2015). For example, shooting of cats in an area where the majority of kills have occurred, or using novel techniques such as toxic implants or toxic collars to take out the rogue animals (Read *et al.* 2015), an approach that draws on some of the early work of Risbey *et al.* (1997) using mouse carcasses impregnated with 1080 oats to take out feral cats. The unilateral removal of foxes where cats are present is unlikely to meet the needs of a fauna recovery project (Glen & Dickman 2005). If cat control is chosen, and if there is some evidence of an individual(s) which displays targeted predatory behaviour, it will be challenging to protect reintroduced prey. Where removal is impractical, we advocate managers reassess the need to undertake a reintroduction, or consider additional or alternative management approaches such as modifying habitat complexity to improve refuge sites and reduce open areas where cats can hunt (McGregor *et al.* 2014, 2015b).

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