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On the right track: placement of camera traps on roads improves detection of predators and shows non-target impacts of feral cat baiting

Michael L. Wysong [A,E], *Gwenllian D. Iacona* [B], *Leonie E. Valentine* [A], *Keith Morris* [C] and *Euan G. Ritchie* [D]

[A]School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[B]Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia.
[C]Science and Conservation Division, Western Australian Department of Biodiversity Conservation and Attractions, 37 Wildlife Place, Woodvale, WA 6983, Australia.
[D]Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, Vic. 3125, Australia.
[E]Corresponding author. Email: mlwysong@gmail.com

Abstract

Context. To understand the ecological consequences of predator management, reliable and accurate methods are needed to survey and detect predators and the species with which they interact. Recently, poison baits have been developed specifically for lethal and broad-scale control of feral cats in Australia. However, the potential non-target effects of these baits on other predators, including native apex predators (dingoes), and, in turn, cascading effects on lower trophic levels (large herbivores), are poorly understood.

Aims. We examined the effect that variation in camera trapping-survey design has on detecting dingoes, feral cats and macropodids, and how different habitat types affect species occurrences. We then examined how a feral cat poison baiting event influences the occupancy of these sympatric species.

Methods. We deployed 80 remotely triggered camera traps over the 2410-km^2 Matuwa Indigenous Protected Area, in the semiarid rangelands of Western Australia, and used single-season site-occupancy models to calculate detection probabilities and occupancy for our target species before and after baiting.

Key results. Cameras placed on roads were ~60 times more likely to detect dingoes and feral cats than were off-road cameras, whereas audio lures designed to attract feral cats had only a slight positive effect on detection for all target species. Habitat was a significant factor affecting the occupancy of dingoes and macropodids, but not feral cats, with both species being positively associated with open woodlands. Poison baiting to control feral cats did not significantly reduce their occupancy but did so for dingoes, whereas macropodid occupancy increased following baiting and reduced dingo occupancy.

Conclusions. Camera traps on roads greatly increase the detection probabilities for predators, whereas audio lures appear to add little or no value to increasing detection for any of the species we targeted. Poison baiting of an invasive mesopredator appeared to negatively affect a non-target, native apex predator, and, in turn, may have resulted in increased activity of large herbivores.

Implications. Management and monitoring of predators must pay careful attention to survey design, and lethal control of invasive mesopredators should be approached cautiously so as to avoid potential unintended negative ecological consequences (apex-predator suppression and herbivore release).

Additional keywords: apex predator, audio lure, dingo (*Canis dingo*), macropodid, mesopredator, occupancy, poison baiting.

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Introduction

There is increasing recognition of the important ecological roles that predators perform (Ritchie and Johnson 2009), and much interest, therefore, in the consequences of managing their populations. Examining how sympatric predators and prey interact with each other and landscape features, and how species respond to perturbations in apex predator activity or abundance, provide important ecological insights, such as what factors shape community structure and dynamics (Ripple *et al.* 2014). This information can also be used to guide more effective pest and wildlife management and conservation (Ritchie *et al.* 2012). However, because of their typically cryptic nature or low densities, or both, predators are often difficult to survey, making it challenging to sample and monitor their populations (Balme *et al.* 2009), and, thus, effectively manage them.

Remotely triggered camera traps have become increasingly popular for use in predator studies because of their ease of deployment, low cost, ability to survey populations for extended periods, and relatively non-invasive nature compared with other wildlife monitoring techniques (Swann and Perkins 2014). Although camera traps can collect data continuously over months to years, securing an adequate sample of individuals for statistical inference can still remain challenging for many predator species (MacKenzie *et al.* 2005; Balme *et al.* 2009). In addition, camera traps, like any wildlife survey method, are prone to imperfect detection, which occurs when detection cannot be separated from abundance, leaving non-detection ambiguous; it is either the result of a species' true absence or a species presence that remains undetected (MacKenzie and Royle 2005). When not properly accounted for in analysis of sampling data, imperfect detection can confound population measures and obscure important ecological patterns and inference (Kellner and Swihart 2014; Dénes *et al.* 2015). Therefore, so as to accurately sample populations of apex predators and determine their effects on sympatric predators and prey, camera-trap surveys need to account for low detection rates (Meek *et al.* 2015) and address imperfect detection (Kéry and Schmid 2004; Burton *et al.* 2015).

Site-occupancy models address imperfect detection by modelling the detection process separate from the ecological parameter of interest and use the estimated detection probability to help estimate the ecological parameter of interest, in this case occupancy (MacKenzie *et al.* 2017). As such, the use of these models is often attractive for the analysis of camera-trapping data. In addition, site-occupancy models do not rely on the identification of unique individuals and, although they cannot provide estimates of abundance, they instead provide an estimate of occurrence, which can be a useful surrogate for abundance and a species' activity in an area, and an informative measure in its own right (MacKenzie and Bailey 2004). In site-occupancy models, occurrence is measured as occupancy (ψ), which is the probability of an area being occupied by a species over the time of the study, and is the result of underlying ecological processes. Detection (p_d), which is the probability of detecting a species given presence, is driven by the observation process and is influenced by habitat features or features of the surrounding landscape that affect local density, movements of individuals, or the efficiency of sampling (Gu and Swihart 2004).

Camera-trap studies that target predators frequently combat the problem of low detection by employing attractants such as baits or lures to draw the target species to the camera for capture, or by placing cameras along specific features such as roads or trails where target animals are likely to travel (Meek *et al.* 2014). Because attractants may increase the efficiency of sampling and roads or trails may influence individual's habitat use and movement, these features are predicted to influence the probability of detection rather than occurrence (Gu and Swihart 2004). Despite the common use of attractants and road- or trail-placed cameras, studies quantifying the effects of these features on species' detectability remains a high priority for camera-trap studies (Burton *et al.* 2015).

Feral cats (*Felis catus*) have had devastating consequences for native wildlife and biodiversity worldwide (Doherty *et al.* 2016). Feral cats can cause population declines directly through predation and indirectly via other means such as disease transmission (Dubey 2008), competition with native predators (Medina *et al.* 2011) and hybridisation (Pierpaoli *et al.* 2003), and they can inhibit the success of fauna reintroduction programs (Moseby *et al.* 2011). Since their arrival to the continent following European colonisation (Koch *et al.* 2015), feral cats have been implicated as a major factor responsible for the extinction or endangerment of many terrestrial vertebrates (Woinarski *et al.* 2019). Reducing the impacts of feral cats on native wildlife is, therefore, essential for the conservation of Australian biodiversity and the re-establishment of threatened fauna populations (Woinarski *et al.* 2014; Doherty *et al.* 2017), and is a key environmental priority of the Australian government (Doherty *et al.* 2019*b*).

Despite the considerable threat that feral cats pose to Australian fauna, controlling their populations effectively, and at appropriate geographic scales, entails considerable challenges (Doherty and Ritchie 2017). Whereas control of feral cat populations can be successful on a local scale through traditional techniques such as trapping, shooting or fencing, landscape-level management has proven more difficult (Doherty *et al.* 2017). Large-scale control of feral cats is especially challenging, given their near-complete occupation of the continent and abundance, which is estimated to range between 2.1 and 6.3 million, depending on variation in rainfall (Legge *et al.* 2017). Recently, two poison baits (*Curiosity*® and *Eradicat*®) have been developed specifically for the lethal control of feral cats in Australia. These baits are generally dispensed aerially at a density of 50 baits km^{-2}, offering the ability to control feral cats over larger areas than is logistically feasible with traditional lethal-control techniques (Doherty *et al.* 2017). Although applications of these baits have shown some success in reducing cat populations on the Australian mainland (Algar *et al.* 2013; Doherty and Algar 2015; Comer *et al.* 2018) or eradicating them on offshore islands (Algar *et al.* 2010), non-target poising remains a risk, despite design features that may limit exposure to some species (Heiniger *et al.* 2018). Importantly, the potential flow-on effects to lower trophic levels from non-target poisoning are not well understood. Because dingoes (*Canis dingo*) co-exist with feral cats over most of their range and are susceptible to poison baiting (Ballard *et al.* 2020), broadcast applications of feral cat poison baits may also reduce and disrupt dingo populations (Wallach *et al.* 2009). As the largest terrestrial apex predator in Australia, aside from humans, the dingo is known to affect prey and mesopredator populations and behaviour (Brook *et al.* 2012; Letnic *et al.* 2012). Although empirical evidence exists to support dingo control of prey (Caughley *et al.* 1980; Pople *et al.* 2000; Letnic and Crowther 2013), the regulation of sympatric competitors remains more contentious (Hayward *et al.* 2015; Nimmo *et al.* 2015). Nonetheless, unintended reduction of dingo populations has the potential to compromise their ecological function, with flow-on effects to lower trophic levels, which could negatively affect biodiversity and threatened species conservation (Wallach *et al.* 2010).

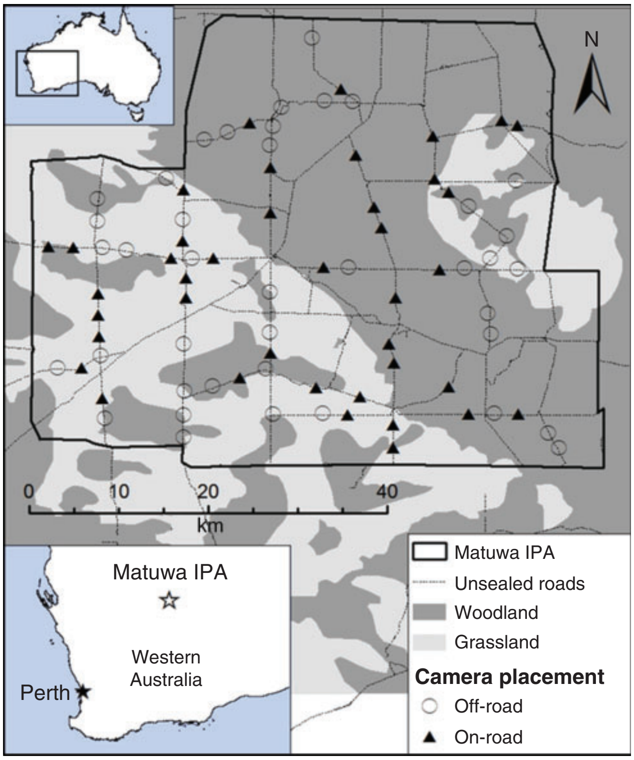

Fig. 1. Location of 78 camera traps deployed during June and July 2013 at the 2410-km^2 Matuwa Indigenous Protected Area in the semiarid interior of Western Australia. Cameras were set a minimum of 1.5 km apart, with an average spacing of 2.73 km ± 1.03 (s.d.) and at least 1 km from the boundary of the reserve. Eighty cameras were set up across the reserve for up to 50 days, resulting in 1407 trap-nights. Maps were created in ArcMap 10.2 (www.esri.com, accessed 7 February 2020).

Here, we examine and quantify the effect that variation in camera-trapping study survey design has for detecting dingoes, their sympatric mesopredator, the feral cat, and two dominant prey species of the dingo, namely, the red kangaroo (*Osphranter rufus*) and the euro (*O. robustus*), in a semiarid conservation reserve in Western Australia. Specifically, we aimed to understand (1) how vehicle tracks and audio lures affect the detection of these target species, as well as (2) how different habitat types, namely, grasslands and open woodlands, affect their occupancy. In addition, we (3) sought to examine the impact of an annual feral cat baiting event on modelled occupancy of cats, dingoes and their prey, while accounting for variable detection.

Addressing these goals will help us implement more effective pest and wildlife monitoring and, hence, deliver better conservation outcomes.

Materials and methods

Study site

The study was conducted in June and July 2013 at the Matuwa Indigenous Protected Area (IPA), a 2410 km^2 reserve located in the semiarid rangelands of Western Australia, 842 km north-west of Perth (26.23°S, 121.56°E; see Fig. 1). The IPA is a former pastoral lease (Lorna Glen) managed jointly by the Wiluna Aboriginal community and the Western Australian Department of Biodiversity, Conservations and Attractions (formerly Parks and Wildlife) since 2000, and at the time of the present study. In 2003, the property was destocked, and recursions are largely prevented by an electric cattle fence along the boundary. This fence presents no barrier to the movement of other medium- to large-sized mammal species in the area, including dingoes, feral cats and kangaroos. Surrounding land uses include active pastoral leases as well as unallocated crown land that receives little to no active management. The application of 1080 poison baits to control dingoes occurs intermittently on some of the surrounding pastoral leases for the purposes of livestock protection. Such uncoordinated and irregular control is unlikely to have a significant impact on dingo abundance over the long term (Allen *et al.* 1996).

The climate is classified as hot, semiarid desert that receives erratic and unpredictable rainfall, averaging 259 mm per year. During the study, annual rainfall was 430 mm. Vegetation communities of the region can be broadly classified as either hummock grasslands, occurring primarily in low-lying sand plains and dominated by spinifex (*Triodia basedoweii* or *T. melvillei*), or open woodlands, occurring in rocky plains or uplands and dominated by mulga (*Acacia aneura*; Beard 1976). Seasonal lakes or claypans with fringing samphire shrublands and halophytic forbs also occur occasionally at the study site. There is a total of 852 km of unpaved, minor vehicular tracks (hereafter simply ‘roads’) on the reserve, which receive very little traffic owing to the remoteness of the location. Dingoes and feral cats are common at the study site, whereas European red foxes (*Vulpes vulpes*) are rare.

Feral cat baiting and camera-trap design

Aerial dispersal of toxic sodium monofluroacetate (1080) *Eradicat*® baits (Western Australian Department of Biodiversity Conservation and Attraction’s bait manufacturing facility, Harvey, WA, Australia) to control feral cats began at the study site in 2003 and has been conducted once annually every year since. Baits are distributed aerially at the density of 50 baits km^{-2} during the cool, dry winter period when the activity of feral cat prey (small mammals and reptiles) is at its lowest; hence, bait uptake is predicted to be the highest (Burrows *et al.* 2003). Evaluation of feral cat track counts from the first 7 years of this baiting program (2003–2009) has shown some success in reducing feral cat activity at least in the short-term, with activity typically dropping substantially in the first few months following baiting, but increasing in subsequent months. This increased activity peaks by about 6 months after baiting and is likely to be due to reinvasion associated with natal recruitment (including possible compensatory breeding) and juvenile immigration from outside the baited area (Algar *et al.* 2013). The present study deployed camera traps before and after the 2013 aerial application of poison *Eradicat*® baits, which occurred in early July over a 4-day period. A non-baited control site and replication of the treatment was not possible because of the operational nature of the study.

We deployed 80 passive infrared motion detector and night-time infrared illuminator cameras (Reconyx Hyperfire PC900; RECONYX, INC., Holmen, WI, USA) throughout the reserve in June 2013. Cameras were deployed for a total of 60 days, representing an 18-day pre-baiting period, and a 32-day post--baiting period, with a 10-day resting period in between, during which the cameras were still active, but the data were not used in analyses. The duration of the resting period was based on movement data from radio-collared feral cats at the study site, which suggests that the last individual to die from toxic-bait ingestion did so 9 days following the start of the aerial bait deployment (Wysong *et al*. 2020). The longer post-baiting deployment was aimed to provide sufficient time to capture any potential behavioural responses of macropodids to changes in dingo activity or abundance. Cameras were spaced a minimum of 1.5 km apart, with an average spacing of 2.73 km ± 0.12 (s.e.) and at least 1 km from the boundary of the reserve (Fig. 1). We chose this spacing to maximise the survey area, while maintaining a camera-trap density that was high enough to capture target predators on the basis of known home ranges in the region (Burrows *et al.* 2003), yet low enough to minimise the possibility of spatial autocorrelation from repeat captures of the same individuals.

Cameras were randomly assigned to two treatments, each comprising two factors. A road treatment involved the placement of cameras either on or off any minor unsealed road, whereas a lure treatment used either an attractant in association with the camera or else left the camera with no lure (Fig. 1). Sample sizes were equal ($n = 20$) for each of the four possible combinations of treatments and factors (i.e. on-road–lure, on-road–no lure, off-road–lure, off-road–no lure). The attractant was the same for all cameras assigned this treatment and consisted of a battery-operated audio lure designed to attract feral cats by producing a chirping sound at a non-regular interval to mimic the call of a distressed baby bird. This lure was chosen because it has been used for leg-hold trapping of feral cats at the study site with some success. The lure was placed ~5 m directly in front of the camera, staked to the ground, and covered with a small amount of vegetation. Camera locations were determined by generating random points along any of the minor unsealed roads on the property by using a random point generator in ArcGIS (ArcGIS 10.2; ESRI, Redlands, CA, USA).

Road-placed cameras were set 1 m off the road and the field of vision was angled 45 degrees across the road to increase the likelihood of capturing fast-moving species (Meek *et al.* 2015). Cameras assigned to off-road treatments were placed ~125 m off the road, which is a distance that has been shown to be independent of any road effects among other carnivore species (Srbek-Araujo and Chiarello 2013). Sites for these cameras were selected so that the field of view and detection zone of the camera would not be obstructed by vegetation (Fig. 2). Habitat type at each camera was classified broadly as either grassland or open woodland, by using available geographic information system data files for the Australian National Vegetation Information System (Executive Steering Committee for Australian Vegetation Information 2003) and the soil-landscapes of Western Australia (Tille 2006). Although vegetation in these two major habitat types is generally sparse, understorey vegetation such as grasses can restrict the field of view of cameras placed low to the ground. To overcome this, we placed all cameras at a height of 100 cm and angled them slightly (~5°) downward.

Cameras were oriented towards the southern half of the sky to avoid interference from the sun during sunrise and sunset, and were programmed to take three consecutive photos when the sensor was triggered, with no delay between images or sets; trigger sensitivity was set at high and night mode at balanced. Photographs were examined and species identified using Camera Base 1.6.1 (Tobler 2007), an Access-driven program that reads the date and time information from the EXIF data of batch-imported photos.

The time interval between successive photographs of dingoes and feral cats showed a peak for elapsed times below 10 min and then dropped off sharply to a distinct low by 30 min. Therefore, we defined 'independent captures' as those separated by 30 min or more unless individuals were distinguishable below this threshold. It was not always possible to distinguish between the two macropodid species, the red kangaroo and the euro; therefore, we identified these species only to genus.

To determine independent photo captures we followed the procedure of Brook *et al.* (2012) and plotted histograms of the time interval between successive photographs for each targeted species at each camera. Captures of target animals showed a peak for elapsed times below 10 min and then dropped off sharply to a distinct low by 30 min.

Analysis

We calculated the pre- and post-bating relative activity index (RAI), which is the total number of independent photo events per 100 camera trap-nights (O'Brien 2011), for all species or groups of species that could be reliably identified. We also calculated naïve occupancy (number of camera-trap sites occupied) before and after baiting for dingoes, feral cats and macropodids.

To visually examine the impact on our target species from *Eradicat*® baiting, we calculated the normalised differential RAI at each camera-trap site before and after baiting for feral cats and dingoes, and for macropodids and dingoes, and mapped these results using ArcGIS. To calculate the differential RAIs, we subtracted dingo RAI from feral cat RAI, and subtracted dingo RAI from macropodid RAI, at each site, and then normalised these values. This produced differential RAI values between –1 and 1 for each comparison (feral cats vs dingoes; macropods vs dingoes) at each camera site, where negative values indicate a net larger dingo RAI and positive values indicate net larger feral cat or macropod RAI.

To analyse the influence of roads and lures on detection, and habitat type and baiting on occurrence of our target species, we used single-season occupancy models for each target species, using the full deployment period of each camera excluding the resting period, discretising the capture data daily. Models were fitted in R using the package 'unmarked' version 0.10-6 (Fiske *et al.* 2010) and ranked in relation to their likelihood using model selection (Burnham and Anderson 2002). With the two covariates each for detection and occupancy, we produced a combination of 16 possible models for each species, including a null model. We did not have any *a priori* expectations of interactive effects of any of the covariates; so, we did not include interactions in the models.

We used the global occupancy model (p(lure+road), ψ(bait+habitat)) to test our hypotheses associated with detection and occupancy, by using 95% profile likelihood confidence intervals. In these models, habitat was assigned a value of one for grassland or a value of zero for no grassland, which by default was open woodland. This allowed for occupancy estimates to be interpreted with respect to one habitat type (i.e. grassland) and enabled us to examine their effects on occupancy. Model estimates were back-transformed to calculate detection probabilities and percentage

Fig. 2. Examples of habitat types and camera-trap set up at Matuwa Indigenous Protected Area. The left column illustrates examples from grassland habitats, whereas the right column illustrates examples from open woodlands. The first row shows examples of each habitat. The second row illustrates a camera set up for cameras placed on and off roads. Cameras are set 100 cm above the ground, angled 45° across roads and slightly down (~5°), and generally set in open areas when not set up on roads. The third row illustrates the field of view from camera captures for each habitat.

occupancy for each target species. We then compared detection probabilities for all four combinations of treatment (road placement) and factor (lure use) and compared percentage occupancy between the two habitats, namely, grassland and open woodland, for each target species before and after baiting.

To examine the extent of spatial autocorrelation in the data (Zuur *et al.* 2009), we examined the spline correlograms constructed from the residuals of the full fitted model and the coordinates of camera placements for each species, by using the R package ncf. version 1.1-5 (Bjornstad 2009).

Ethics statement

All field methods were conducted in accordance to procedures that were approved by the University of Western Australia

Animal Ethics Committee (RA/3/100/1277) and the Western Australian Department of Biodiversity Conservation and Attractions Animal Ethics Committee (DPaW AEC 2013-21).

Results

A total of 797 independent photo captures occurred over 3683 camera trap-nights, and recorded 25 identifiable mammal and bird species, with 17 captures that could not be identified (see Table S1, available as Supplementary material to this paper) for details of all species detected and their relative activity indices). Over the total deployment period, there were 75 independent photo captures of dingoes, 66 of feral cats and 342 of macropodids. Two camera traps failed (one on-road–no-lure and one on-road–lure) and were not included in the analysis.

During the study, 28.2% of camera-trap sites were occupied by dingoes before baiting and 19.2% (9% less) were occupied post-baiting; for feral cats, 20.5% were occupied pre-baiting and 24.4% (~4% more) post-baiting, whereas, for macropodids, these naïve occupancies were 34.6% pre-baiting and 53.8% (~19% more) post-baiting. Feral cat RAI decreased at 14 sites following baiting but increased at 11 sites following baiting. Dingo RAI decreased at 22 sites and increased at three sites, whereas macropodid RAI decreased at 16 sites and increased at 30 sites post-baiting.

The mean normalised differential RAI (±s.e.) between feral cats and dingoes was −0.12 (±6.5 × 10^{-2}) before baiting, and 0.12 (±9.4 × 10^{-2}) following baiting, indicating a greater feral cat RAI than dingo RAI following baiting (net RAI = +0.24). The mean normalised differential RAI between macropodids and dingoes was 0.11 (±5.8 × 10^{-2}) before baiting and 0.22 (±3.8 × 10^{-2}) following bating, indicating a greater macropodid RAI than dingo RAI following baiting (net RAI = +0.11). Dingo RAI was greater than feral cat RAI at 16 sites before baiting, but greater than feral cat RAI only at seven sites following baiting. Dingo RAI was greater than macropodid RAI at 11 sites before baiting, but greater only at four sites following baiting (Fig. 3).

The results of model selection for the 16 competing occupancy models for each of the three target species showed that the global model was among the top-performing models (ΔAIC of <2) for dingoes (ΔAIC = 1.73) and macropodids (ΔAIC = 1.97), but not for feral cats (ΔAIC = 3.68; Table 1). Examination of spline correlograms indicated that spatial autocorrelation was not present in the data (see Fig S1, available as Supplementary material to this paper).

Effects of lures and roads on detection

The placement of cameras on roads was a significant factor for detecting dingoes and feral cats, but not macropodids, whereas the use of audio lures was not a significant factor affecting detection for any of the target species (Fig. 4). The back-transformed probabilities of detection estimates were slightly

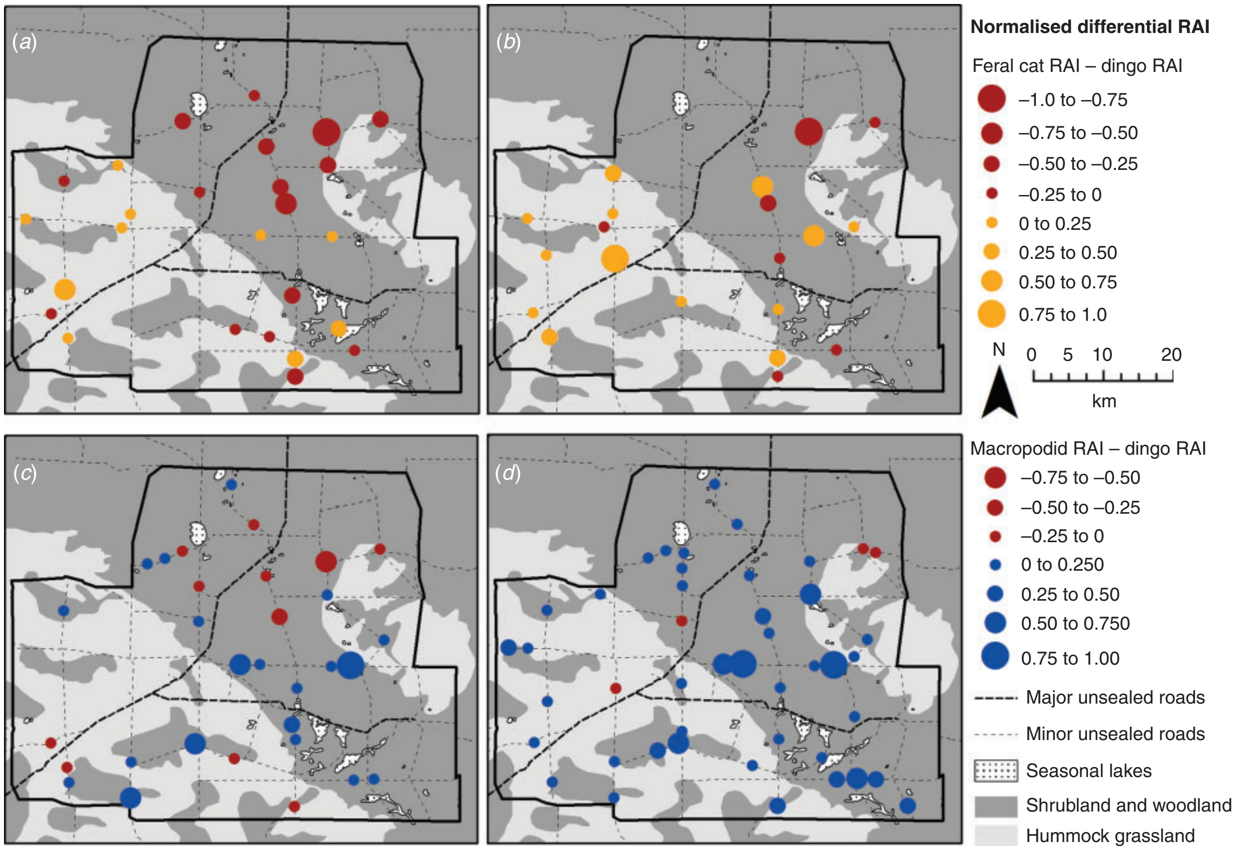

Fig. 3. Normalised differential relative activity index (RAI) between feral cats and dingoes (*a*) before baiting and (*b*) after baiting and between macropodids and dingoes (*c*) before baiting and (*d*) after baiting.

higher for all species when lures were used. For feral cats and dingoes, the probability of detection was much higher for cameras placed on roads than for cameras placed off roads, whereas for macropodids, the probability of detection was similar regardless of camera placement on or off road (Fig. 5, Table S2).

Table 1. Akaike information criteria (AIC) and model weights for the top competing single-season site-occupancy models (within ΔAIC = 2) and the global and null models

Models are constructed from camera-trapping data for the three target species at Matuwa Indigenous Protected Area

Species and model	AIC	ΔAIC	Weight
Cat			
p(lure+road),ψ(.)	555.69	0.00	0.31
p(road),ψ(.)	556.65	0.96	0.20
p(lure+road),ψ(bait)	557.52	1.83	0.12
p(lure+road),ψ(habitat)	557.54	1.86	0.13
p(lure+road),ψ(bait+habitat)	559.37	3.68	0.05
p(.),ψ(.)	594.95	39.26	0.00
Dingo			
p(road),ψ(bait+habitat)	530.88	0.00	0.65
p(lure+road),ψ(bait+habitat)	532.61	1.73	0.28
p(.),ψ(.)	597.53	66.64	0.00
Macropod			
p(lure),ψ(bait+habitat)	1535.65	0.00	0.34
p(.),ψ(bait+habitat)	1536.84	1.19	0.19
p(lure+road),ψ(bait+habitat)	1537.54	1.89	0.14
p(.),ψ(.)	1569.28	33.63	0.00

Effects of habitat and baiting on occupancy

Habitat type was related to the occupancy of dingoes and macropodids, but not feral cats (Fig. 4). Specifically, grasslands had a negative effect on the occupancy of dingoes and macropodids, and open woodlands had a positive effect. Cat baiting negatively affected dingoes and positively affected macropodids, but had no significant effect on feral cat occupancy. Across both habitats, post-baiting occupancy estimates for feral cats were only slightly lower than were pre-baiting estimates; however, for dingoes, these differences were much greater, with occupancy estimates being much lower following baiting. Macropodid post-baiting occupancy estimates were much greater than were pre-baiting estimates for both habitats (Fig. 5, Table S3).

Discussion

Our study has provided the type of information that is needed to design effective sympatric predator-monitoring and -assessment programs. We showed that on-road cameras positively affect the detection of dingoes and feral cats, and open woodlands positively affect the occupancy of dingoes and macropodids. Within this context, a broad-scale application of poison baits, targeted for feral cat population control, did not negatively affect feral cat occupancy, but, rather, it is likely that it resulted in reduced dingo occupancy and was associated with an increased occupancy of their main prey (macropodids). Our results suggest that

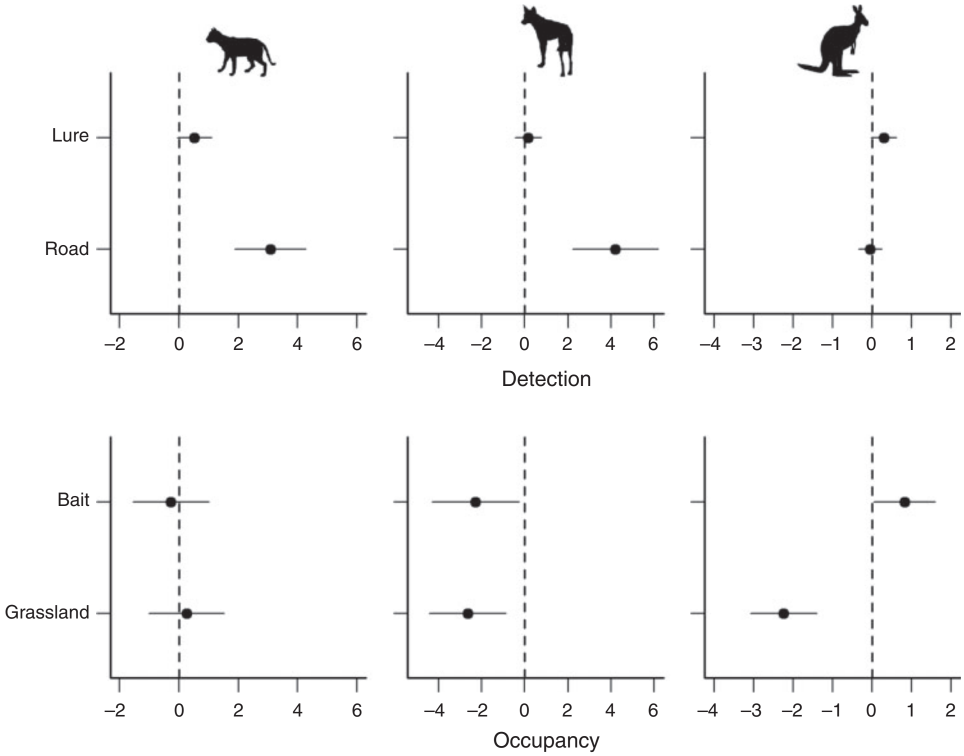

Fig. 4. Parameter estimates with 95% confidence intervals from the global occupancy model (p(lure+road),ψ(bait+ habitat)) for target species at Matuwa Indigenous Protected Area.

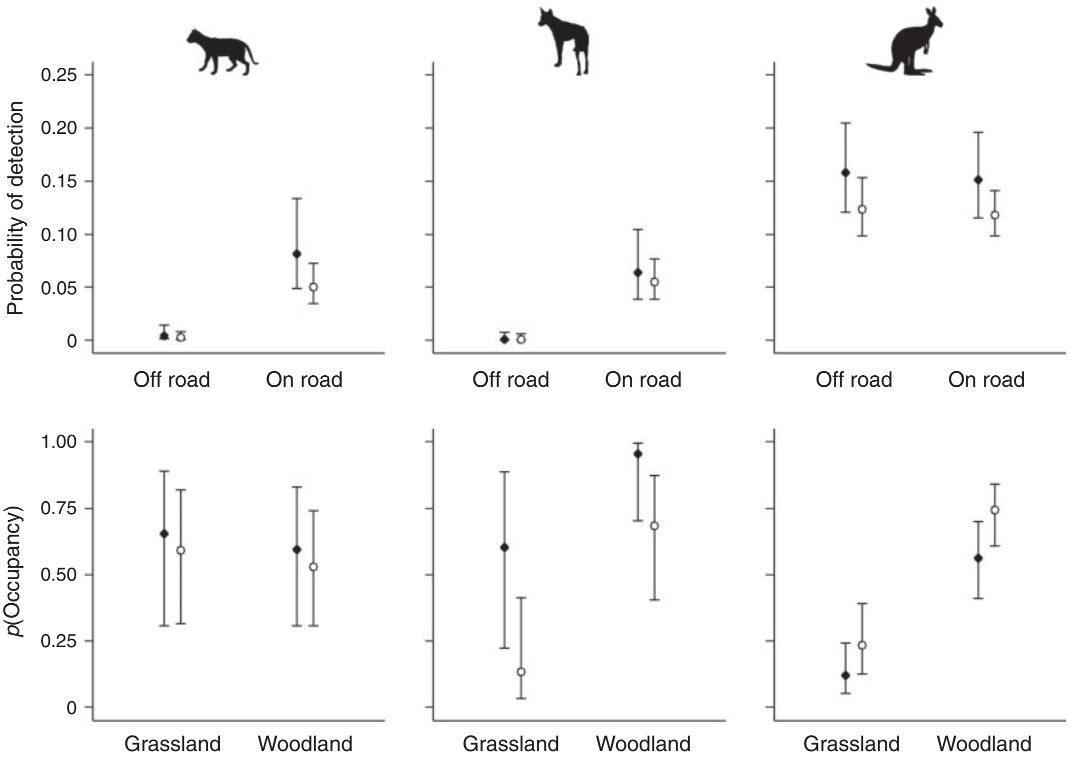

Fig. 5. Detection and occupancy estimates for (*a*) feral cats, (*b*) dingoes and (*c*) macropods derived from camera-trap data at Matuwa Indigenous Protected Area. Detection estimates are for cameras placed on and off roads where black circles indicate cameras with lures and white circles indicate those without. Occupancy estimates are for grassland and open woodland sites, where black circles indicate pre-baiting detections and white circles indicate post-baiting detections. Error bars are 95% confidence intervals.

where adequate road networks exist, surveys for predators may be greatly enhanced by the placement of camera traps on or in very close proximity to roads. Such improved survey design may help collect larger samples of population information of cryptic predators or predators with a low abundance and, in doing so, enhance understanding of species interactions and the potential consequences of predator–prey management.

Camera-survey design and species detection

The probability of detecting dingoes from road-placed cameras was 64 and 61 times higher than that from cameras placed off road when lures were included and not included respectively. For feral cats, this difference was 20 and 21 times higher (Fig. 5). This large effect of linear features on the detection of predators in camera-trap studies is well documented globally (Larrucea *et al.* 2007; Harmsen *et al.* 2010; Sollmann *et al.* 2012; Srbek-Araujo and Chiarello 2013; Cusack *et al.* 2015). In Australia, several studies have demonstrated higher capture rates of dingoes, feral cats and foxes from road-based cameras than from off-road camera sets (Towerton *et al.* 2011; Wang and Fisher 2012; Read *et al.* 2015; Raiter *et al.* 2018). Our findings are consistent with these studies and support recommendations for the deployment of cameras on roads or trails to achieve higher carnivore-detection rates (Meek *et al.* 2014).

Although non-significant, our estimates of detection probability were generally higher with lures for both predator species, as well as for macropodids (Fig. 5). Studies investigating the effect of audio lures on detectability are rare for most ecosystems and species globally (Rocha *et al.* 2016). In a semiarid region of South Australia, Read *et al.* (2015) found that audio lures did not increase photo captures of dingoes and feral cats but that they did elicit behavioural responses from them, and Moseby *et al.* (2004) found that the proportion of survey sites visited by feral cats was significantly greater for sites that used audio lures. A study by Stokeld *et al.* (2015) from northern Australian tropical savannas found no effect of lure type, including audio lures, on the detection of feral cats and that cats showed little behavioural interest in any lure type. Given the non-significant but positive results of the effect of audio lures on detection, it seems reasonable to assume that the use of audio lures may attract predators to camera traps but that any benefit of increased detection from their use is likely to be insignificant compared with the benefit from deploying cameras in a very close proximity to or on roads.

Habitat type and species occupancy

Dingo and macropodid occupancies were significantly higher in open woodlands than in grasslands. Apex predators are likely to select habitats on the basis of where their preferred prey are more abundant and easier to capture (Stephens and Krebs 1986; Pike *et al.* 1999; Spong 2002; Milakovic *et al.* 2011). In semiarid regions of Australia, the two macropodid species in our study typically prefer open woodlands to hummock grasslands (Short *et al.* 1983). Therefore, it is likely that the higher dingo occupancy in open woodlands is driven by the occurrence of their main prey.

Feral cat occupancy was not significantly affected by habitat, despite the higher occupancy of dingoes in open woodlands. Competing species may coexist through partitioning in diet, space use or temporal activity (Gause 2019). In arid Australia, dingoes and feral cats tend to consume different prey (Doherty *et al.* 2015*a*; Doherty *et al.* 2019*a*). A high degree of diet partitioning has been observed at our study location (Wysong *et al.* 2019); therefore, dietary competition between the two species is low. It is also possible for mesopredators to co-exist with apex predators while avoiding them temporally or at finer spatial scales (Schuette *et al.* 2013; Fancourt *et al.* 2015; Wang *et al.* 2015; Torretta *et al.* 2016), and this has been documented for dingoes and feral cats in other parts of Australia (Brook 2013). As such, a lack of strong competition for prey, as well as temporal and fine-scale spatial avoidance, may facilitate the co-occurrence of these two predator species, and allow feral cats to exploit both habitats equally. However, we caution that our data are limited in their ability to understand causal relationships between dingoes and feral cats, and it is also possible that dingoes do not exert a strong influence on feral cat space use during the particular environmental conditions (above-average rainfall) during which our study occurred (Greenville *et al.* 2014).

Impacts of poison baiting on cats and sympatric species

Feral cat occupancy was not significantly affected by the broad-scale application of *Eradicat*® poison baits designed to target them, despite small reductions in their occupancy within both habitats. Using measures of relative activity from track counts or proportion of radio-collared individuals killed, previous studies have found strong reductions in feral cat populations following baiting (Algar *et al.* 2010; Johnston *et al.* 2011), including at our study site (Algar *et al.* 2013). Although few studies have evaluated the impact of feral cat baiting using site-occupancy models, a study by Comer *et al.* (2018) found that feral cat occupancy was significantly reduced following baiting each year over a 5-year period. The lack of feral cat response to baiting in our study could be due to several factors, including timing of bait application, prey availability, pre-baiting feral cat population levels or lack of bait uptake. It is unlikely that this lack of response is due solely to bait avoidance from bait-wary cats surviving in the population after repeated annual baiting since baiting does not appear to be less effective after each year and because annual reinvasion following baiting is high due to the open nature of the study site (Algar *et al.* 2013). It is possible that the higher-than-average rainfall recorded during the study period contributed to greater prey availability for feral cats and, thus, reduced uptake of poison baits (Christensen *et al.* 2013). Our study highlighted that poison baits may not be successful in reducing feral cat populations in every baiting application (Moseby and Hill 2011; Doherty and Algar 2015) and that a multi-year baiting program, in conjunction with other control measures (e.g. trapping, shooting), may be necessary to observe and sustain a long-term reduction in feral cat population size (Doherty and Ritchie 2017).

Despite there being minimal impact on feral cats, our results suggest that a significant impact on dingo occupancy occurred in association with the application of *Eradicat*® baits (Fig. 4); dingo occupancy decreased by 78.0% in grasslands and 28.5% in open woodlands. The application of poison baits to control dingo populations is routinely used across much of Australia for the purpose of protecting livestock (Fleming *et al.* 2006). Therefore, it is not surprising that dingoes would also be affected by poison baits designed for feral cat uptake, especially considering that one *Eradicat*® bait contains enough 1080 toxin (4.5 mg) to deliver a lethal dose to an adult dingo (Fleming *et al.* 2001). However, when feral cat poison baits have been deployed in areas where dingoes also occur, there has been little evaluation of the non-target impacts on dingo populations (Algar *et al.* 2013; Comer *et al.* 2018). Our results show the potential for impacts on dingo populations from the application of feral cat poison baits, and underscore the need for consideration of non-target risks from baiting programs designed for feral cats (Buckmaster *et al.* 2014).

We also found a significant increase in macropodid occupancy following *Eradicat*® baiting; 96.2% in grasslands and 32.3% in open woodlands (Fig. 5). An increase in the activity or abundance of prey can be triggered by the removal or reduction of the population of their main predator, and this is either the result of a numerical or behavioural response to reduced predation pressure and risk (Creel and Christianson 2008). Given the short time frame in our study, it is most likely that the observed increase in macropodid occupancy following baiting was the result of a behavioural response of macropodids to the post-baiting reduction in dingo occupancy, that is, a relaxation of the landscape of fear (see Ritchie and Johnson 2009), and not of a change in macropodid population size. Several studies have reported negative correlations between macropodid and dingo activity or abundance (reviewed by Letnic *et al.* 2012). Using passive tracking stations, Colman *et al.* (2014) found that macropodid abundance was consistently greater in sites where dingo populations were controlled by 1080 baiting. Similarly, Leo *et al.* (2019) found that the abundances of nailtail wallabies and kangaroos, determined from spotlight surveys, were greater at sites where 1080 baiting occurred than at sites where no baiting occurred. Our study is consistent with these studies and, to our knowledge, is the first to experimentally link a baiting program specifically designed to target feral cats to an increase in macropodid activity via a non-target reduction of a dingo population.

We acknowledge that our study did not have a non-baited control and, as such, we can infer only that the reduction in dingo occupancy was the result of the baiting event. Reduced dingo occupancy could have been caused by seasonal behavioural and movement variation associated with whelping, which typically occurs between mid-May to mid-August for dingoes in our study region (Thomson 1992). During this time, movements of breeding females may be restricted and avoid areas commonly used by humans, such as roads, but the extent of area over which non-nursing individuals move is not likely to vary from that at other times of the year (Thomson 1992). However, in support of our explanation for increased herbivore activity post-baiting, results of a GPS-collaring program at the study site in 2014 found that 4 of 16 collared dingoes died within 5 days of the beginning of a 3-day *Eradicat*® baiting application and these deaths were attributed to the ingestion of the toxic baits (M. L. Wysong, unpubl. data). Therefore, it seems likely that the reduced dingo occupancy following baiting is at least partially the result of the baiting event, and probably affected herbivore space use and activity.

Conclusions and management implications

Our study emphasises the importance of camera trap-survey design in facilitating improved understanding of ecological relationships between predators and prey. By deploying camera traps on roads, we greatly increased the detection probabilities for cryptic predators (dingoes and feral cats) and obtained enough data to investigate ecological questions regarding their habitat use and impacts from lethal predator control. However, audio lures did little to increase the detection of target predators. Because camera traps are often much more difficult and time consuming to set up far away from roads and the use of lures may also require additional time and costs to deploy, cameras deployed on roads without lures have the added benefit of significant cost-savings for research and management programs. Therefore, where possible and consistent with the study objectives, we recommend an emphasis on road placement of cameras to enhance detection of predators. However, we caution that road deployments have issues with increased likelihood of theft and may require additional equipment such as locked camera housing (Meek *et al.* 2013).

The application of poison baits to target feral cats in Australia is a relatively new management tool compared with traditional lethal control techniques such as trapping and shooting. Whereas most applications of these baits have focussed on controlling feral cats in areas where dingoes either do not co-occur (Algar *et al.* 2010; Johnston *et al.* 2011; Moseby and Hill 2011), or else, occur in low numbers (Doherty and Algar 2015), the expansion of the use of these baits to areas where feral cats co-occur with dingoes presents a significant risk for non-target impacts on dingoes. Non-target impacts on dingoes from baiting could result in increased activity or abundance of feral cats relative to dingoes, which may expose small- and medium-sized prey to greater feral cat depredations (Wysong *et al.* 2019). Although we did not measure herbivory in our study, an increase in herbivore populations as a result of apex predator suppression could lead to a greater grazing pressure on vegetation (Schmitz *et al.* 2000) and reduced cover for threatened species, making them more susceptible to feral cat predation (Doherty *et al.* 2015*b*; Geary *et al.* 2019).

Our study has provided important insights for the management of feral cats using poison baits where they co-occur with dingoes. At our study site, dingo occupancy was significantly higher in open woodlands than grasslands, whereas feral cat occupancy was not affected by habitat type. Therefore, to reduce the risk of unintended non-target and negative ecological consequences of broad-scale poison-bait application, and, hence, poor conservation outcomes, we recommend limiting the deployment of feral cat baits to grasslands and using a rigorous camera trap-surveying program to evaluate the impact of the baiting on feral cats and other sympatric predators and prey. We encourage invasive predator-control programs elsewhere to also consider similar complexities within their local contexts.

Conflicts of interest

The authors declare no conflicts of interest.

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