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WILDLIFE RESEARCH

Fox and cat responses to fox baiting intensity, rainfall and prey abundance in the Upper Warren, Western Australia

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ABSTRACT

Context. Invasive predators are major drivers of global biodiversity loss. Red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) have contributed to the decline and extinction of many native species in Australia. The deployment of poison baits to control fox populations is a widespread conservation tool, but the effects of baiting intensity, rainfall and prey abundance on baiting effectiveness remain poorly understood. **Aims.** We aimed to understand what influences the association between fox baiting intensity, red fox activity and feral cat activity, to provide inferences about what might affect the effectiveness of fox baiting in reducing fox activity. **Methods.** We used generalised linear models to assess how fox and cat activity changes in relation to fox baiting intensity, rainfall, native prey availability and distance to agricultural land over a 6-year period (2006–13) in the forest ecosystems of the Upper Warren region of south-western Australia. **Key results.** We found that fox activity was negatively associated with rainfall in the previous 12 months and positively associated with prey abundance and fox baiting intensity. We also found an interaction between fox baiting and prey abundance, with fox activity increasing with prey activity in areas of low and moderate baiting intensity, but remaining constant in areas of high baiting intensity. Feral cat activity was positively associated with prey abundance and fox baiting intensity. We found no clear relationship between fox and cat activity. **Conclusions.** The drivers of the association between fox baiting and fox activity are unclear because intense fox baiting was targeted at areas of known high fox abundance. However, our results indicate that intense fox baiting may be effective at decoupling the positive association between fox activity and prey abundance. Our results also suggest a positive association between fox baiting intensity and feral cat activity, thus supporting the case for integrated fox and cat management. **Implications.** We caution interpretation of our results, but note that management of invasive predators could be improved by adjusting the intensity of management in response to changes in environmental conditions and local context (e.g. strategically conducting intense predator management where prey abundance is highest). Improved understanding of these associations requires a monitoring program with sufficient replication and statistical power to detect any treatment effects.

Keywords: critical weight range, feral cat, impact evaluation, invasive predator control, lethal control, pest management, predator–prey, red fox.

Introduction

Invasive mammalian predators are major drivers of species' declines and extinctions globally (Doherty *et al.* 2016). Their impacts have been greatest on islands where prey are naïve to the threat of novel predators (Salo *et al.* 2007; Medina *et al.* 2011). Reducing the impacts of invasive predators on biodiversity is a key priority for conservation managers across the globe (Lodge *et al.* 2006; Russell *et al.* 2015). However, threat management interventions do not always lead to positive conservation outcomes for native biodiversity (Walsh *et al.* 2012), and effectiveness can be limited by factors such as the presence of natural and anthropogenic disturbances and/or co-occurring invasive species (Prior *et al.* 2018). The ability to effectively mitigate a threat and subsequently improve target biodiversity values is an important source of uncertainty in conservation resource allocation (Nicol *et al.* 2019). Understanding the contexts in which invasive predator management effectively reduces predator densities and distributions, and subsequently mitigates their impacts on biodiversity, will help to ensure actions are targeted where and when success is likely to be greatest (Benshemesh *et al.* 2020).

In Australia, red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) are a major threat to native wildlife and especially mammals (Woinarski *et al.* 2015; Kearney *et al.* 2019). Reducing predation by cats and foxes on vulnerable prey is therefore a key priority for conservation practitioners, researchers and the broader community. Lethal control through shooting, trapping and poison baiting is the most common management approach. Millions of dollars are spent on lethal control in Australia each year (Reddiex *et al.* 2007). Poison baiting of foxes is commonly implemented at the landscape scale across large parts of southern and eastern Australia. This can be highly effective at reducing fox densities and has led to increases in the abundance of some prey species, particularly threatened mammals (Dexter and Murray 2009; Wayne *et al.* 2011; Hunter *et al.* 2018). However, there are instances where species that were expected to benefit from fox control continued to decline following the implementation of poison baiting programs, such as the southern brown bandicoot (*Isoodon obesulus*) in south-western Victoria (Robley *et al.* 2019) and the long-nosed bandicoot (*Perameles nasuta*) in Booderee National Park, New South Wales (Lindenmayer *et al.* 2018), suggesting that the baiting in these locations is not effectively reducing fox density to a level where these species can persist, or that other factors are limiting their populations (Hunter *et al.* 2018).

The success of conservation actions can be affected by stochastic events and other abiotic and biotic drivers, including fire and weather (Maxwell *et al.* 2019). For example, rainfall has an important influence on the outcomes of invasive predator management in Australia (Tulloch *et al.* 2020). Aerial baiting of feral cats in Western Australia's Gibson Desert was most successful at reducing cat abundance during periods of low rainfall when the availability of prey was limited (Burrows *et al.* 2003). Drought conditions also influenced the success of a poison-baiting scheme in south-eastern Australia by reducing predation pressure on vulnerable forest-dwelling species (Claridge *et al.* 2010). In contrast, drought prior to a predator control program to protect the yellow-footed rock-wallaby (*Petrogale xanthopus*) reduced the ability of wallabies to recover due to competition for food resources between the wallabies and other invasive species not affected by the baiting program (goats and rabbits) (Sharp and McCallum 2015). High rainfall prior to or during poison control has negatively influenced outcomes because it can lead to greater plant productivity and irruptions of herbivorous prey species, such as mice, which are preferentially eaten over baits (Priddel and Wheeler 1997; Priddel *et al.* 2007; Johnston *et al.* 2012; Tulloch *et al.* 2020). Evaluation of the outcomes of conservation actions therefore needs to be placed in appropriate geographic, environmental, and temporal contexts because the success of management actions is not uniform over space and time (Tulloch *et al.* 2020).

Lethal fox control has been occurring in the Upper Warren region of south-western Australia for over 40 years to reduce the impacts of predation on threatened species, e.g. the woylie (*Bettongia penicillata ogilbyi*). It is suspected that, at least in some parts of the south-west, the long-term reduction of fox numbers through baiting may have led to increases in feral cat abundance and predation of critical-weight-range mammals (35–5500 g mass) by cats, due to feral cats being similar sized predators and likely in competition with red foxes (Marlow *et al.* 2015; Wayne *et al.* 2017). Feral cats also do not regularly consume baits targeted at foxes (Dundas *et al.* 2014). Here, we assess changes in the activity of feral cats and red foxes in relation to changes in fox baiting intensity, rainfall, prey availability, and distance to agricultural land over a 6-year period (2006–13) in the Upper Warren. Our primary predictions are as follows:

1. Given fox abundance and occupancy can be negatively affected by lethal fox control (Hunter *et al.* 2018), we expect that fox reporting rate (i.e. the number of days foxes were detected at a sand pad, divided by total survey days) would decrease in response to increasing spatial and temporal intensity of lethal fox baiting;
2. Some evidence suggests that fox baiting is most effective following periods of low rainfall and prey availability (Short *et al.* 1997; Burrows *et al.* 2003; Claridge *et al.* 2010), so we expect that the effectiveness of baiting at reducing fox reporting rate will be highest during periods of low rainfall; and
3. Because feral cats can increase in abundance as a result of effective fox control (Marlow *et al.* 2015; Stobo-Wilson *et al.* 2020) and above average rainfall (Legge *et al.* 2017), feral cat reporting rate will be positively related to increased fox baiting intensity and/or reduced fox activity, and these relationships will be strongest following periods of low rainfall.

Methods

Study area

The Upper Warren region of south-western Australia includes 140 000 ha of publicly managed native vegetation (Wayne *et al.* 2013). It has a mediterranean climate, with warm summers, cool winters and mean annual rainfall of ~650–1000 mm (BoM 2020). The dominant habitat types are eucalypt forests and woodlands, dominated by jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and wandoo (*E. wandoo*) trees. Fire is a prominent disturbance in the region, with regular prescribed burns and occasional wildfires (Boer *et al.* 2009). Most of the study area has been subject to one or more native timber harvesting events over the last 100 years, and although most land is now classified as either a Nature Reserve or National Park, about a third of the area is State Forest and remains available for timber harvesting until 2024 (Wayne *et al.* 2006).

Red foxes and feral cats have been present in the region since at least the early 20th century (Abbott *et al.* 2014), and have contributed to the decline of multiple threatened species (Abbott 2008; Wayne *et al.* 2017). Since 1977, fox control has been implemented across the region at varying levels of intensity, ranging from irregular ground baiting to frequent aerial baiting. The frequency and extent of baiting across the region expanded significantly in the 1990s, moving to annual or twice-yearly frequencies. Quarterly aerial baiting began in 1997 across the region as part of the Western Shield program and still operates today. Since 1995, part of the study region has also had ground baiting applied at quarterly intervals (Fig. 1). In 2009, a portion of the study region switched to ground baiting applied at monthly intervals (Fig. 1), providing an opportunity to assess the impact of increased intensity of ground and aerial baiting on foxes and cats. An important consideration in the context of this study is that the choice of locations for increasing baiting frequency were not random – they were chosen based on prior knowledge of high abundances of small and medium sized mammals (e.g. woylie, numbat (*Myrmecobius fasciatus*), chuditch (*Dasyurus geoffroii*)) and high abundances of foxes, likely confounding the interpretation of baiting intensity and invasive predator activity. We take this into account when interpreting our results. Because feral cats rarely take fox baits (Dundas *et al.* 2014), it is not expected that the long-term fox baiting has had any direct effect on feral cat activity.

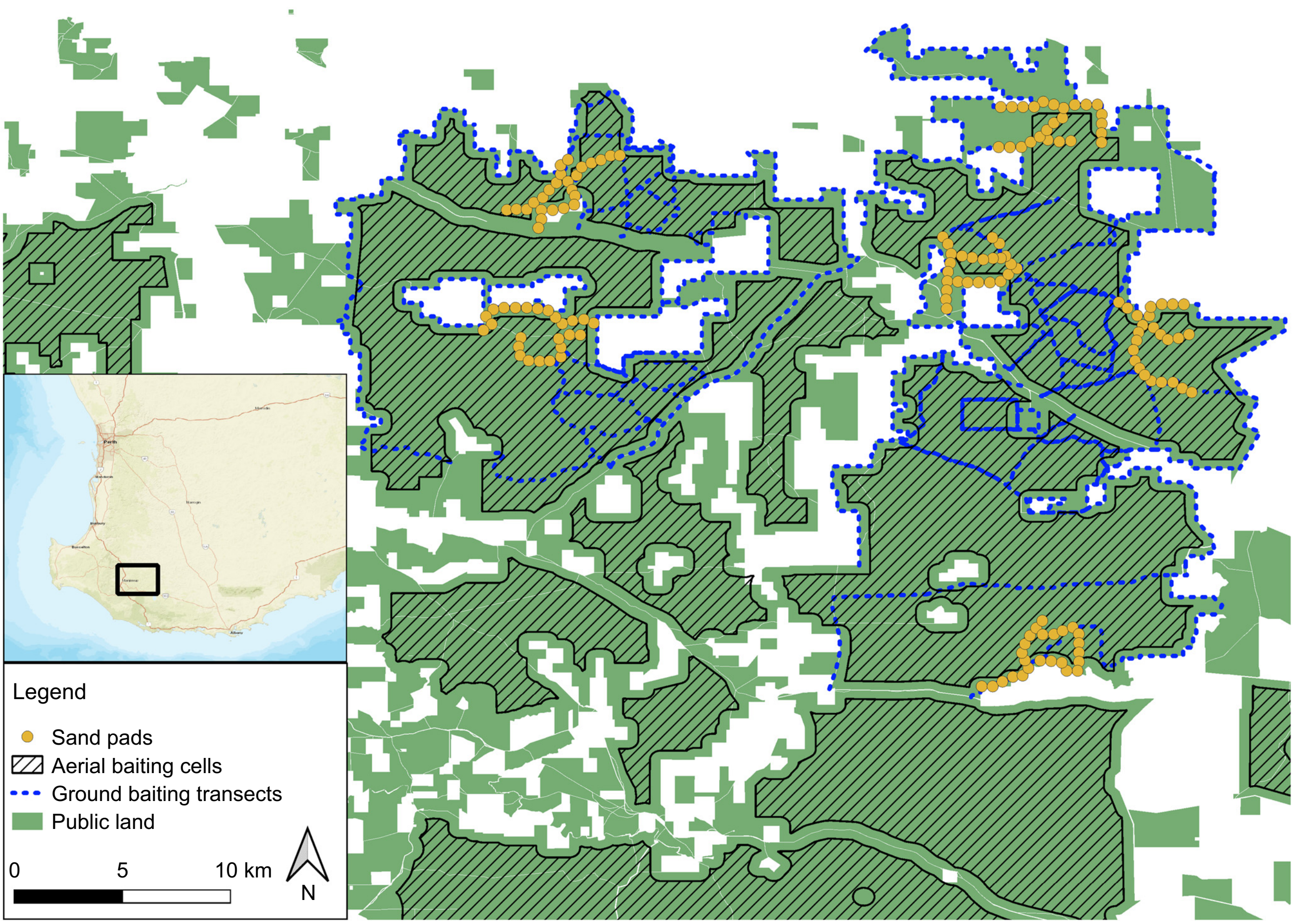

Fig. 1. Map of study area in the Upper Warren, south-western Western Australia. Yellow circles indicate the sand pads on each of the six transects. Shaded green areas indicate areas of public land dominated by forest. Black hashed areas are the areas subject to quarterly aerial baiting, and the blue dashed lines show the ground baiting transects across the study region. Inset shows the study area (black rectangle) in the broader south-western Western Australia region.

Field surveys

From 2006 to 2013, five transects of 25 sand pads spaced at 500-m intervals were regularly monitored (Fig. 1). From 2010 to 2013, a sixth transect of 25 sand pads was also monitored. Transects were separated by 4–30 km each. Each sand pad was constructed by removing soil from a 1 × 4-m wide area on a vehicle track and replacing that channel with sand suitable for reading animal footprints. Throughout the study period, each sand pad transect was surveyed once each in spring and autumn each year. Surveys were also conducted opportunistically throughout the study period at some transects. To account for this variation in survey effort in analysis, we broke the surveys up into 21 distinct sessions over which to model activity dynamics.

Each sand pad survey was conducted for at least 4–6 nights, and up to 10 nights. All fauna activity (i.e. tracks) detected on each pad each night was recorded each morning with a confidence rating for print identification (1 = certain, 2 = probable, and 3 = possible). Only prints marked as certain (1) were used in analysis for this study. Probable (2) detections made up only 1% of fox detections and 4.4% of cat detections, so excluding these detections was not expected to affect any results. Foxes and cats were marked as present at a sand pad if at least one track was detected on a given sampling occasion (day). Where tracks had been disturbed by vehicles, rain, etc. the data from that sampling occasion was not considered in the models (i.e. marked as NA in the detection history). Where more than 10 pads were considered 'disturbed' on a given day, the entire transect was removed from the dataset for that sampling occasion.

From the sand pad detection data, we calculated the reporting rate of fox and cat detections at each sand pad, during each survey session, as an index of activity. To account for uneven sampling effort, the reporting rate for each species was the number of survey days each species was detected at a sand pad, divided by the total number of included survey days for that sand pad. Reporting rate has advantages over traditional occupancy or presence/absence metrics because it is typically more sensitive to changes in abundance of predators (Nimmo *et al.* 2015). To illustrate change in the reporting rate of each species over time, we plot the smoothed reporting rate as a function of Julian date for each transect using a generalised additive model with five knots and a binomial error distribution.

Covariate development

The density of predator baits deployed can vary spatially due to the spatial configuration of habitat, land tenure, and road access (ground baits), and temporally due to a range of factors (e.g. weather, contractor availability). Because this spatial and temporal variation in intensity likely influences the effect of baiting on target species (Hradsky *et al.* 2019), we calculated a spatially and temporally explicit baiting intensity metric to include in our models. Baiting intensity was calculated by collating baiting records from across the study period that included the number of baits laid, the dates they were laid, and the spatial footprint over which the baits were laid – either bait station points buffered by 2 km (ground baiting; 2 km chosen based on typical fox home range size in similar environments [see Table S1 of Carter *et al.* (2012)], or polygons of treatment areas (ground baiting and aerial baiting). These were then used to calculate a baiting intensity metric (number of baits per km^2) across the study region within a 12-month period prior to the date of each survey. Given the relatively large home range of foxes and cats, rather than calculating a sand pad-specific baiting intensity for a given survey session, we extracted the baiting intensity value at each sand pad point and then calculated the mean baiting intensity for each transect across the 25 sand pads for that session. Therefore, each individual transect had a unique baiting intensity value for each session which was used in the models.

To assess the relationship between predator activity and rainfall, which may influence overall food and shelter resources including both native prey and agricultural subsidies, we calculated rainfall variables at each site using daily precipitation mapped grids for the entire survey period from the Australian Bureau of Meteorology (BoM 2020). These daily 1-km grids were then summed across the dates spanning 12 months prior to each survey to provide maps of the amount of precipitation across the study region in the specified time periods. These values were then extracted for each sand pad location to provide sand pad-specific estimates of the amount of rainfall in the previous 12 months prior to each survey. We used a 12-month window because this is a sufficiently large window for foxes and cats to respond numerically to rainfall-driven changes in resources (Greenville *et al.* 2014), and 12-month rainfall lags often correlate with temporal changes in the abundance of species (Lindenmayer *et al.* 2019).

To assess the relationship between predator activity and small and medium-sized prey resources, we calculated a prey capture rate (the pooled capture rate of a subset of potential prey species [e.g. woylie, brushtail possum, chuditch and quenda] in the Upper Warren) using the dataset described in Wayne *et al.* (2017). Because not all transects were surveyed frequently enough to calculate these metrics for each survey at each transect, we built a generalised additive model (GAM) to interpolate capture rates between surveys. This meant that we could derive transect and session-specific (i.e. spatially and temporally explicit) estimates of prey abundance for use as covariates in our models. The GAM was fitted with a single term of 'date' (the number of days since the first date of the first survey session; range 0–2394) interacting with transect, with a limit of 11 knots to allow flexibility in the model while avoiding overfitting. The GAM was then used to predict capture rates across all dates and transects. To validate whether the GAM was appropriately predicting capture rates in periods with few data, we used *k*-fold cross-validation with 10 randomly assigned folds to assess the predictive capacity of the models. Predictive capacity was assessed using the mean squared error. To account for variation in the assignment of the folds, we calculated a bootstrapped estimate of MSE, using 100 replicates and present the mean MSE and standard error (Table A1).

Finally, we calculated the distance to the nearest non-native vegetation across the study region using the inverse of mapped native vegetation extent in the region (DPIRD 2020). We then excluded all land parcels smaller than 5 ha to remove small areas mapped without native vegetation, because these are unlikely to strongly influence fox and cat activity. Because it was difficult to distinguish between plantations and cleared landscapes given the dynamic nature of land use in the region, our distance to the nearest non-native vegetation includes pasture, cropped land and plantations of non-native eucalypt and pine. This map was then checked visually to ensure consistency with satellite imagery and local knowledge. To calculate the distance to the nearest agricultural land, we measured the distance between each sand pad point and the nearest identified patch of non-native vegetation in R, using the *sf* package (Pebesma 2018).

To ensure that all covariates used in the modelling of predator activity were not highly correlated ($r_s < 0.7$), and thus could be included in the same model, we calculated the Spearman correlation coefficients for each pair of covariates (Table A2). The full set of covariates used in each of the sub-models and their hypothesised relationship are outlined in Table 1.

Predator activity modelling

To identify the drivers of red fox and feral cat reporting rate at the sand pad scale (number of days detected vs not detected at each sand pad) throughout the study period, we used generalised linear models with binomial error distributions. For red foxes, we fitted models with all additive combinations of baiting intensity in the previous 12 months, rainfall in the previous 12 months, distance to agriculture and prey abundance (Table 1). To further understand the relationship between fox activity and baiting intensity, we also tested for interactive effects between baiting intensity and prey abundance, rainfall and distance to agriculture in a separate model selection process. For feral cats, we used the same set of covariates but also included fox reporting rate. All models included an autoregressive temporal autocorrelation structure (AR1) to account for sampling sessions occurring close together in time, grouped by site to account for repeat sampling of sites. All candidate sets included a null model with only random effects.

To identify the most parsimonious model within each species' candidate set, we used an information theoretic approach, using Akaike's information criterion adjusted for small sample size (AICc). We considered that the model with the lowest AICc was the most highly ranked and those within two AICc of the top-ranked model as strong candidates (Burnham and Anderson 2002). The most highly ranked models were checked for overdispersion ($\phi > 1.5$), which can arise through higher than expected variance in the model (Quinn and Keogh 2002). To evaluate how well the most highly ranked models fitted the data, we calculated the variance explained by the fixed effects (marginal R^2; Nakagawa and Schielzeth 2013). Analyses were conducted using the packages *mgcv* (Wood 2012) and *MuMin* (Barton 2021). Full results of the model selection process can be found in the Appendix.

Results

Red fox

Red fox activity was highly variable across the study period (Fig. 2). The most parsimonious model for red fox occurrence included a negative relationship with rainfall in the previous 12 months (Fig. 3*a*, Table 2), a positive relationship with baiting intensity in the previous 12 months (Fig. 3*b*, Table 2) and a positive relationship with prey abundance (Fig. 3*c*, Table 2). The most parsimonious fox model had a low marginal pseudo *R*-squared value of 0.07 (Table 2). Of the models of fox activity that tested different interactions between fox baiting intensity and other variables, the most parsimonious model had an interaction between baiting intensity and prey abundance (Fig. 4, Table 2). This model showed a positive association between fox activity and prey abundance in areas of low and moderate fox-baiting intensity, and no association between fox activity and prey abundance in areas of high baiting intensity (Fig. 4, Table 2).

Feral cats

The most parsimonious model for feral cat occurrence included a positive relationship with baiting intensity in the previous 12 months (Fig. 5*a*, Table 2) and a positive relationship with prey abundance (Fig. 5*b*, Table 2). Fox reporting rate and distance to agriculture were not identified as informative predictors. The most parsimonious feral cat model also had limited explanatory power, with a pseudo marginal *R*-squared value of 0.05 (Table 2).

Discussion

Evaluating the efficacy of management actions to reduce or eliminate a pest species is a critical component of best practice pest management and effective ecosystem management (Baylis *et al.* 2016). Another key dimension is to consider and evaluate how the success of actions can be affected by stochastic factors such as weather and disturbance (Tulloch *et al.* 2020). In the Upper Warren region of south-west Australia, we found that

Table 1. Predictor variables used in model selection process for red fox and feral cat statistical models, descriptions of the variables and predicted relationship with each species' sub-model.

Variable	Description	Hypothesised relationship
Baiting intensity	The number of fox baits laid per km^2 in the 12 months before the time of survey. This includes ground baiting transects along roads, which were buffered by 2 km, and aerial baiting which was conducted over the entire study area on public land, except within 0.5 km of private land	Negative relationship between fox reporting rate and baiting intensity due to fox baiting killing foxes (Hunter *et al.* 2018) Positive relationship between cat reporting rate and baiting intensity due to fox baiting killing foxes, therefore reducing pressure on cats by foxes (Marlow *et al.* 2015)
Rainfall	The total rainfall (mm) calculated at each transect in the 12 months prior to the first occurrence of the survey. Calculated using the daily Bureau of Meteorology climate grids (BoM 2020)	Positive relationship between rainfall and fox activity because rainfall increases would generally lead to an increase in food resources (small prey, macropods, agricultural resource subsidies) (Greenville *et al.* 2014; Scroggie *et al.* 2018) Positive relationship between rainfall and cat activity because rainfall increases would generally lead to an increase in food resources (small prey, macropods, agricultural resource subsidies) (Greenville *et al.* 2014)
Mean prey capture rate	The mean prey trap capture rate at a transect in the 12 months prior to the date of the first occasion of each survey session. Calculated using capture data for species such as woylies, brushtail possums, southern brown bandicoot and western quoll captures (i.e. a subset of potential fox prey species) from Wayne *et al.* (2017)	Positive relationship between mean prey capture rate and both fox and cat activity, as they may be tracking these prey species over time (Arthur *et al.* 2012)
Distance to non-native vegetation	The distance (km) from each sand pad site to the nearest area of non-native vegetation (includes tree plantations, grazing and cropping land). Areas of non-native vegetation were identified using mapped native vegetation in the region	Negative relationship between distance to non-native vegetation and both fox and cat activity as both predators may be getting food subsidies from agricultural areas, and so would be in higher abundance closer to edges of non-native vegetation (Hradsky *et al.* 2017)
Fox	Fox reporting rate for each transect and session	Negative relationship between cat activity and fox activity as cats can avoid foxes in space and time (Marlow *et al.* 2015)
Transect	The transect that the sand pad survey was conducted at, one of Balban, Boyicup, Keninup, Moopinup, Warrup and Winnejup	Activity will be variable over space
Year	The year that the survey was conducted (2006–13)	Activity will be variable over time

fox activity was positively related to baiting intensity and prey abundance, and negatively related to rainfall. We also found an interaction between fox baiting and prey abundance. By contrast, feral cat activity was positively related to baiting intensity and prey abundance. However, interpretation and extrapolation of these results must consider the confounded design, whereby areas of increased fox baiting intensity were also areas of known high fox activity.

Both fox and cat activity were positively related to prey abundance in the 12 months prior to survey, and the relationship between fox activity and fox baiting appears to decouple in areas of high prey abundance. This relationship suggests that invasive predator populations may be tracking overall prey abundance across the Upper Warren region – selecting areas where there is greater access to food. Given that red foxes are generalist carnivores (Davis *et al.* 2015; Fleming *et al.* 2021), it was expected that activity would be positively related to a general prey abundance index as observed here. A concurrent diet analysis from the study region found that, aside from sheep, foxes did not focus on any specific prey species, consuming a broad range of vertebrates, invertebrates, and fruits (Wayne *et al.* 2013). Therefore, the positive correlation seen here may also be due to our prey abundance index being positively associated with high productivity sites more generally, rather than foxes tracking the specific prey species included in our index. Because foxes and cats are more likely to use sites with higher prey availability, and high baiting intensity appears to decouple this relationship in our study, intense fox control efforts in these areas should continue and methods for cat control should continue to be explored.

We found that red fox activity was highest when rainfall was relatively low (e.g. <550 mm in the previous 12 months), or baiting was relatively intense (e.g. >16 baits/km^2 in the previous 12 months). The positive association between fox activity and baiting intensity is likely a reflection of the study's management focus, whereby areas in which baiting intensity increased were areas known to have greater fox activity and threatened species abundance. The effectiveness of poison baiting may also be lower when rainfall occurs shortly after bait deployment because precipitation hastens deterioration of the bait and toxin (Gentle *et al.* 2007). Although we found no evidence of an interactive effect of baiting intensity and rainfall, rainfall-driven baiting success/effectiveness has been observed in other parts of Australia (Burrows *et al.* 2003; Claridge *et al.* 2010). The overall

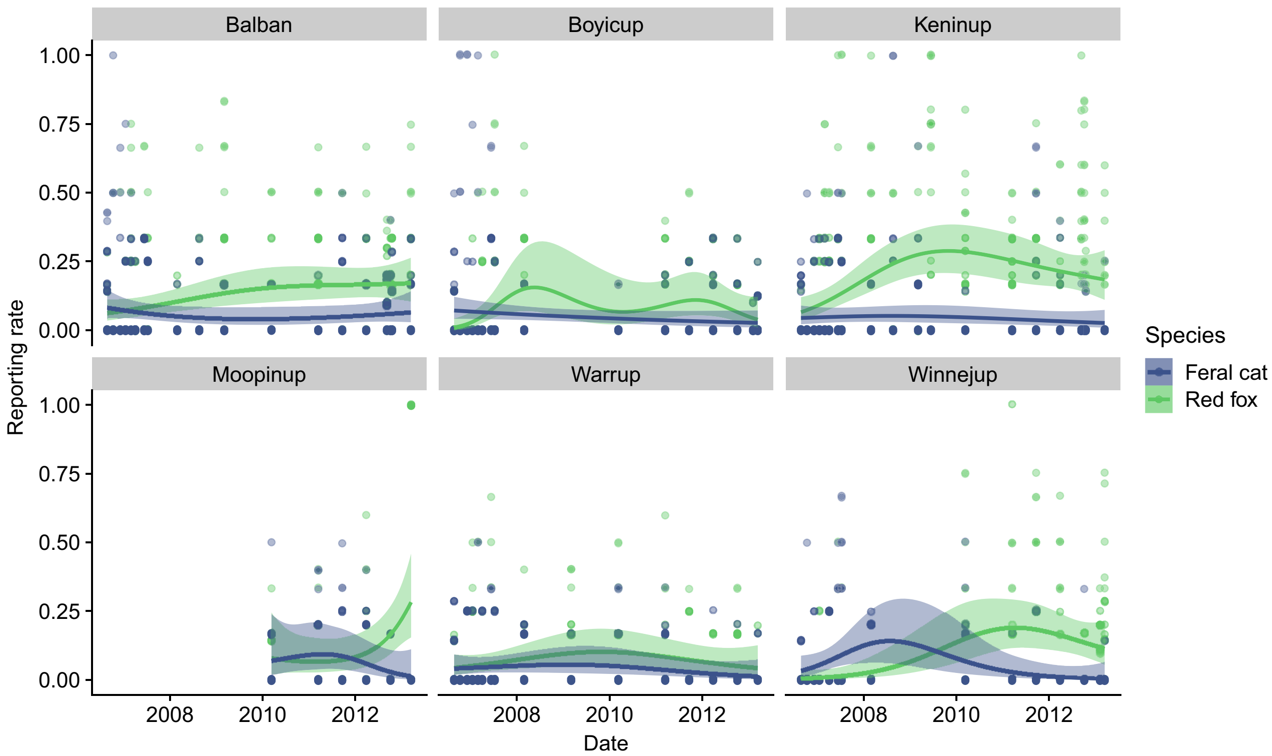

Fig. 2. Plot of sand pad-level reporting rates for each trapping session and smoothed mean predictions for red foxes and feral cats. Lines and ribbons show the smoothed means and 95% confidence intervals, and points are the reporting rates for each sand pad at each time of sampling.

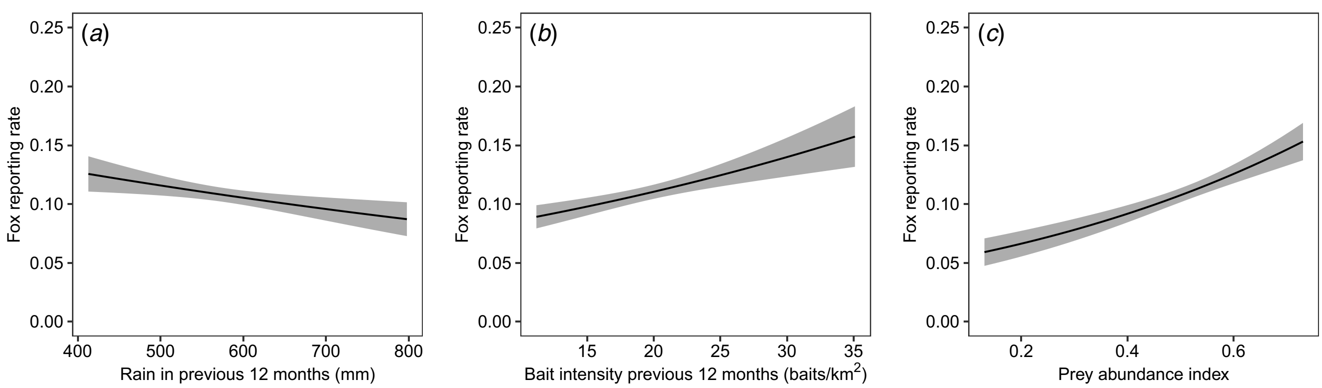

Fig. 3. Predicted red fox reporting rate relationships with (*a*) rainfall in the previous 12 months, (*b*) baiting intensity in the previous 12 months and (*c*) prey abundance. Shaded areas show the 95% confidence intervals.

positive relationship between fox activity and baiting intensity may also be influenced by rapid recolonisation of baited areas by surviving individuals from less frequently baited or unbaited neighbouring areas (Newsome *et al.* 2014; Kämmerle *et al.* 2019).

We also found that feral cat activity was highest when both fox baiting intensity and prey abundance were high. The release of cats from suppression by a larger predator (in this case, the red fox) is hypothesised as a major driver of woylie declines in the Upper Warren (Wayne *et al.* 2017) and mammal declines elsewhere in southern Australia (Marlow *et al.* 2015; Robley *et al.* 2019; Cunningham *et al.* 2020). These results suggest that it remains a plausible driver in the Upper Warren; however, it is also possible that higher cat activity is due to behavioural changes that result in cats being detected on sand pads more frequently (e.g. increased use of roads), rather than increased abundance. Regardless, management approaches that simultaneously control red foxes and feral cats may be required to reduce the impacts of invasive predators on species of concern

Table 2. Table of coefficient estimates, standard errors, 95% confidence intervals and pseudo R^2 values for the most parsimonious model in each of the three model candidate sets, including the fox model set, the fox interaction model set and the cat model set.

Model	Covariate	Estimate	s.e.	95% confidence intervals		Marginal R^2
				Lower	Upper	
Fox	**Intercept**	−2.11	0.03	−2.17	−2.04	0.07
	Rainfall	−0.09	0.03	−0.15	−0.02	
	Bait intensity	0.15	0.03	0.08	0.21	
	Prey	0.25	0.04	0.18	0.32	
Fox interaction	**Intercept**	−2.18	0.04	−2.25	−2.11	0.08
	Bait intensity	0.05	0.04	−0.03	0.13	
	Prey	0.24	0.04	0.17	0.32	
	Bait intensity × Prey	−0.12	0.03	−0.18	−0.06	
Cat	**Intercept**	−3.06	0.05	−3.15	−2.97	0.05
	Bait intensity	0.21	0.05	0.12	0.30	
	Prey	0.10	0.05	−0.01	0.20	

Rainfall refers to the amount of rainfall (mm) in the 12 months prior to trapping, baiting intensity refers to the transect-scale baiting intensity in the 12 months prior to each trapping session, and prey refers to the transect-scale mean prey abundance in the 12 months prior to trapping. Bolded covariates are those with 95% confidence intervals that do not overlap zero.

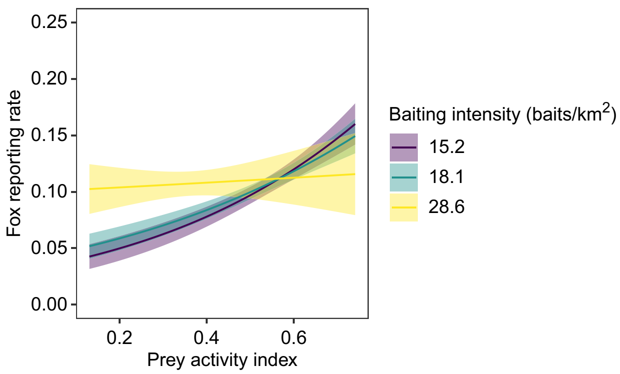

Fig. 4. Predicted red fox reporting rate relationships with an interaction between baiting intensity in the previous 12 months and prey abundance in the previous 12 months. Shaded areas show the 95% confidence intervals. Baiting intensity values represent the 10th, 50th and 90th percentiles of fox baiting intensity (baits per km^2) in the 12 months prior to each survey period.

(Marlow *et al.* 2015; Comer *et al.* 2020). This remains a difficult proposition, given the effectiveness of lethal cat control methods at the landscape scale is highly variable between years and locations (Christensen *et al.* 2013; Comer *et al.* 2020; Doherty *et al.* 2022). To date, effective broadscale control of feral cats in temperate environments has been demonstrated in subtropical, mediterranean and arid ecosystems through aerial baiting programs, but the effectiveness is inconsistent (Comer *et al.* 2018, 2020; Lohr and Algar 2020). In places where broadscale feral cat baiting is ineffective, including areas with high and reliable food availability, alternative approaches may be required for effective and sustained control of feral cats and protection of key areas (e.g. refuges) and wildlife populations. One option is grooming traps that automatically shoot a poison onto cats and and do not rely on low food availability to be effective (Moseby *et al.* 2020).

Testing the association between fox baiting and fox activity was complicated by the increase in baiting intensity occurring in locations known to have high fox and prey abundance. Further, because the changes in reporting rate over the course of the study were highly variable and may not be correlated directly with abundance, the relationships among foxes, cats and poison baiting are difficult to interpret. The variable reporting rates, low variance explained by the highest ranked models (<0.10 R^2), and the lack of unbaited areas to serve as controls in this study (a typical issue for large-scale baiting programs that specifically aim to cover as broad an area as possible and conserve threatened species) are important considerations for the interpretation of these results.

Monitoring predators with sufficient power to detect changes in abundance, rather than site occupancy or use, in response to management interventions is difficult (Bal *et al.* 2018; Geyle *et al.* 2020). The present study focuses on changes in fox and cat activity using sand pads, but changes in baiting intensity may impact predator abundance/density more strongly than predator activity. Activity, abundance, and density estimates for low density carnivores are generally correlated (Clare *et al.* 2015), but presence/absence data are typically less sensitive to drivers of population change (e.g. lethal control) than density and abundance (Linden *et al.* 2017). Although this study is based on a historical dataset that used sand pad monitoring, camera trapping is now a

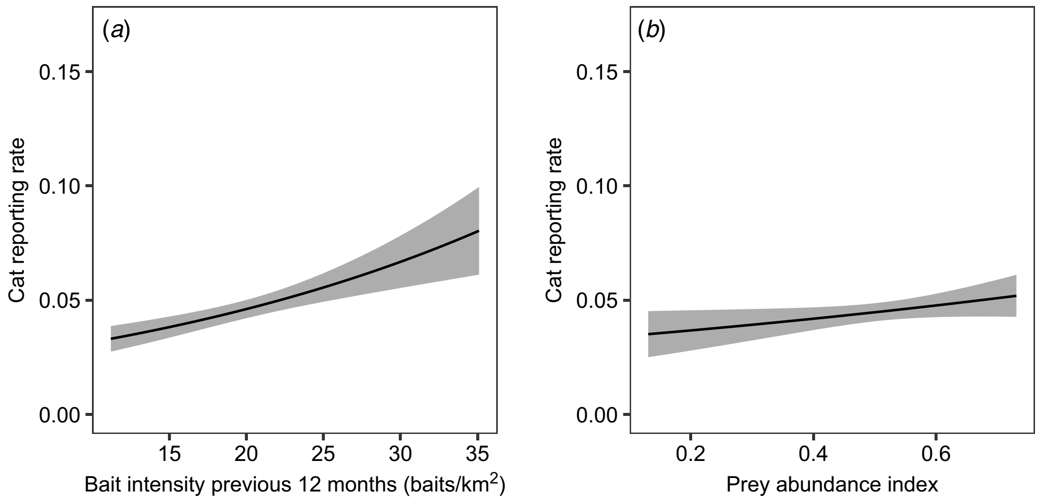

Fig. 5. Predicted feral cat occurrence relationships with (*a*) baiting intensity in the previous 12 months and (*b*) prey abundance. Shaded areas show the 95% confidence intervals.

preferred method for passive monitoring of predators (Meek *et al*. 2015). Monitoring designs that use multiple approaches (e.g. GPS tracking, DNA metabarcoding, camera or live trapping and diet analysis), and provide robust abundance or density estimates of the species being managed and the species of conservation concern, are therefore required to appropriately evaluate the outcomes of invasive predator management (Le Pla *et al*. 2022).

Our study suggests that invasive predator management should rarely be 'set-and-forget.' Rather, managers may need to adjust effort and intensities of actions according to external drivers such as weather (e.g. rainfall) and biotic factors (e.g. prey abundance), and monitor the outcomes with sufficient statistical power in order to maximise outcomes for biodiversity. Our results point to additional complexities influencing the effectiveness of fox baiting, suggesting whole-of-ecosystem approaches are necessary to fully disentangle how invasive predator management can be successful into the future.

Supplementary material

Supplementary material is available online.

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Data availability. Data and code used in this study are available at https://github.com/billygeary/upperwarren_foxcat.

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