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Assessing target and non-target species interactions with buried non-toxic meat baits across fire mosaics

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ABSTRACT

Context. Lethal 1080 baiting to control invasive predators, or to reduce livestock predation by canids, is a widespread management tool used throughout Australia and New Zealand. Techniques to reduce the impact of 1080 baiting on non-target species exist, but their efficacy, including effects of environmental variation and disturbance on baiting outcomes, remains poorly understood. **Aims.** We aimed to experimentally quantify the extent to which target and non-target species dig up and consume buried baits, and to examine how habitat variation and fire affect such interactions. **Methods.** Remote cameras were deployed for 70 days to monitor the fate of non-toxic baits in the semi-arid Big Desert-Wyperfeld region of southeastern Australia. Species digging up or eating baits (collectively 'bait interactions') were identified, and the effects of environmental factors on bait interaction rates were assessed. **Key results.** Non-target species accounted for 128 (88%) of 146 total bait interactions, primarily native mice species. Target species interacted with fewer baits and took longer to record bait interactions, with foxes (*Vulpes vulpes*) averaging 41 days for 17 bait interactions and one dingo (*Canis familiaris/Canis dingo*) taking 60 days, whereas native mice interactions occurred after ~13 days. At sites where foxes and dingoes were detected, both target species almost always interacted with baits (83%), whereas non-target species interacted with baits at less than half of the sites they were detected (42%). Areas with greater variation in fire frequency (pyrodiversity) and mid-successional vegetation were associated with more native mice-bait interactions. **Conclusions.** Non-target species interacted with baits more often and sooner than target species, suggesting efforts to reduce predator populations could have inadvertent effects on other species. The influence of fire and vegetation variables on bait interaction rates also highlights the importance of accounting for landscape features when designing lethal control programs. **Implications.** Predator control can benefit native wildlife, and help to reduce livestock loss; however, managers must account for environmental factors that may influence which species are most likely to be affected by toxic baits, and by extension possible broader impacts on ecosystems. Monitoring to assess baiting outcomes and limit the negative consequences for non-target species constitutes best practice.

Keywords: Dingo, European red fox, fire management, invasive species control, integrated ecosystem management, lethal predator control, non-target impacts, pyrodiversity, sodium fluoroacetate (1080).

Introduction

Lethal control of animal populations through poison baiting is a widespread tool used in threatened species conservation, pest management, and for reducing human-wildlife conflict (reviewed in Taggart *et al.* 2023). Invasive and native predators can have detrimental effects on agricultural production of crops and livestock and/or on native wildlife and ecosystems (Saunders *et al.* 2010; Capizzi *et al.* 2014; Doherty *et al.* 2016). Predator management often centres on lethal control with poison baiting for the protection of agricultural production values and threatened species (Reddiex *et al.* 2006; Philip 2019; Taggart *et al.* 2023). Various substances have been trialled for use in lethal baiting, but sodium fluoroacetate (hereafter: 1080) remains one of the most frequently used toxins for lethal control programs (Taggart *et al.* 2023), especially in Australia and New Zealand.

In Australia, lethal control of animals with poison baiting is common on both private and public lands (Philip 2019). Australia has the most extensive use of poison baiting globally, the majority of which is carried out with 1080 (Taggart *et al.* 2023), primarily targeting dingoes (*Canis familiaris/Canis dingo*) and European red foxes (*Vulpes vulpes*). Governments and private landholders invest tens of millions of dollars in this management action annually (Bomford and Hart 2002; McLeod 2004). The widespread use of 1080 is in part due to the natural occurrence of fluoroacetate in *Gastrolobium* plant species in Australia, primarily in the south-west of the country. The coevolution of *Gastrolobium* and native herbivorous and omnivorous species from this region means native wildlife typically have a relatively high tolerance to this chemical compound (Mead *et al.* 1985). Additionally, the lower basal metabolic rate of marsupial species compared to eutherians (Dawson and Hulbert 1970) may contribute to a higher innate tolerance for the toxin due to a more gradual impact on mitochondrial functioning (Twigg and King 1991). Hence, many introduced and invasive species have a much higher sensitivity to 1080, and as such, 1080 is generally considered moderately target-specific when used to control eutherian species such as foxes, feral cats (*Felis catus*), European rabbits (*Oryctolagus cuniculus*), and dingoes (Calver *et al.* 1989).

There are a range of concerns surrounding the ethics (Littin *et al.* 2014; Wallach *et al.* 2015), efficacy (Dundas *et al.* 2014; Newsome *et al.* 2014; Allsop *et al.* 2017; Kreplins *et al.* 2018) and outcomes (Wallach *et al.* 2009; Marlow *et al.* 2015; Campbell *et al.* 2019; Rees *et al.* 2023) of poison baiting with 1080. In particular, the impact of 1080 baiting on non-target species has been investigated as a cause for concern around its continued use (APVMA 2008). Non-target bait interference is reported in nearly 30% of control program outcomes (Taggart *et al.* 2023). However, monitoring and quantifying the impact of poison baiting on non-target individuals is not routine and can be practically and logistically challenging (Glen *et al.* 2007).

Risks to non-target species from poison baiting remain insufficiently understood (Glen *et al.* 2007; Ross and Eason 2022). Some species, such as the spotted-tailed quoll (*Dasyurus maculatus*) and eastern quoll (*Dasyurus viverrinus*), have been the focus of substantial research to determine their risk of unintentional poisoning (Mcilroy 1981; Belcher 1998; Claridge *et al.* 2006). While individual mortalities of quolls exposed to baiting have been recorded, no negative impacts have been demonstrated at a population level (Körtner *et al.* 2003; Murray and Poore 2004; Körtner and Watson 2005; Claridge *et al.* 2021). Most other native species are assumed to be low risk, either due to their body size, sensitivity to 1080, or the relative risk of individual animals encountering and consuming baits when compared to the population-level risk posed by targeted predator species (APVMA 2008).

Despite the presumed low risk of baiting to most non-target species, a number of techniques are recommended or legislated in different jurisdictions across Australia aimed at minimising non-target harm. These 'best practice' baiting methods include – reducing palatability of the bait matrix to non-target species, by using dried, cooked or manufactured meat rather than fresh meat (Allen *et al.* 1989; Calver *et al.* 1989; Saunders *et al.* 1995); injecting blue or green dye into baits to reduce visual appeal for non-target species (particularly birds; Cowan and Crowell 2017); deploying baits in late autumn or early spring, to align with lower activity periods for varanid species (Thomson 1986; Robley *et al.* 2009); and reducing the ability of non-target species to access baits by burying them, either below ground or within a mound of sand/earth to a depth of 10 cm (Allen *et al.* 1989; Thomson and Kok 2002; Saunders and McLeod 2007; Moseby *et al.* 2011). Bait burial 8–10 cm below the surface is a requirement in eastern Australian states including Victoria due to concerns about non-target harm from surface-laid baits (Saunders and McLeod 2007).

How these 'best practice' methods affect the outcomes of baiting programs is not well-established, and when implementing methods like bait burial, reported bait take rates for target species can vary significantly. Reported uptake of buried baits by foxes fluctuates widely, between 1% (Dundas *et al.* 2014) and 35% (Thompson and Fleming 1994; Saunders *et al.* 1999). A similarly broad range of uptake rates has been reported for dingoes across previous studies of buried baits, from <1% (Glen and Dickman 2003*a*; Kreplins *et al.* 2018) to 17% (Allen *et al.* 1989). Non-target species are often reported as relatively unimpacted when baits are buried (Allen *et al.* 1989; Fleming 1996), but in addition to quolls (Belcher 1998; Glen and Dickman 2003*a*), other species that have been reported as capable of digging up baits buried to a depth of 10 cm include corvids (Allen *et al.* 1989; Dexter and Meek 1998), yellow-footed antechinus (*Antechinus flavipes*; Fairbridge *et al.* 2003), brush-tailed phascogales (*Phascogale tapoatafa*; Fairbridge *et al.* 2003), swamp rats (*Rattus lutreolus*; Dexter and Meek 1998), and bush rats (*Rattus fuscipes*; Fairbridge *et al.* 2000). Despite being suggested or required in many Australian states, the efficacy of these baiting methods for actually preventing negative impacts on non-target species is not well understood.

An often-overlooked aspect that may affect baiting outcomes is the influence of environmental factors, including fire history and habitat variation. Many environmental factors have been shown to alter predator behaviour and habitat use, including pyrodiversity (Bliege Bird *et al.* 2018), time since fire (McGregor *et al.* 2014; Bliege Bird *et al.* 2018; Geary *et al.* 2018; Doherty *et al.* 2023), and vegetation complexity (McGregor *et al.* 2014; Hradsky *et al.* 2017*a*; Stobo-Wilson *et al.* 2020). In turn, these factors may also influence and regulate prey populations (Griffiths and Brook 2014; Bennison *et al.* 2018; Nimmo *et al.* 2019; Sukma *et al.* 2019). Despite these effects on predators and prey, there has been limited investigation into the relationship between environmental variation and predator control outcomes for target and non-target species. Lethal predator control is regularly recommended or implemented in response to bushfires and planned burns (Robley *et al.* 2012; DENR 2017; Hradsky 2020), but how fire (and subsequent changes to vegetation) could be altering the outcomes of predator control programs is poorly understood.

We therefore aimed to evaluate the potential for non-target species to be impacted by 'best practice' 1080 bait deployment in a semi-arid mallee ecosystem, through monitoring interactions with replica (non-toxic) meat baits in a simulated canid-control program. We aimed to determine how fire history and vegetation characteristics influence bait uptake rates by target and non-target species. Specifically, we aimed to determine:

(1) Which target and non-target species interact with buried baits.
(2) Whether the relative ratio of interactions with baits compared to detections at bait sites would differ between target and non-target species.
(3) How long after bait deployment target and non-target species would first interact with baits.
(4) How environmental factors (time since fire, pyrodiversity, and vegetation cover) influence target and non-target species interacting with baits.

Based on previously reported target and non-target bait uptake rates, we predicted that foxes (Thompson and Fleming 1994) and dingoes (Allen *et al.* 1989) would primarily interact with baits, and that cats (Moseby *et al.* 2011), corvids (Dexter and Meek 1998), varanids (Moseby *et al.* 2011), and small mammals (Moseby *et al.* 2011) would also interact with buried baits, but to a lesser extent. We also predicted that target species would interact with baits in less time (Fleming 1996), and with greater frequency relative to the number of times they were detected (Thompson and Fleming 1994) than non-target species. Based on observed relationships between environmental variables and animal abundance and behaviour, we also predicted that target species would be more likely to interact with baits in recently burned areas with reduced vegetation cover (Robley *et al.* 2012; Geary *et al.* 2018), and that non-target species may be more likely to interact with baits in long-unburned (Griffiths and Brook 2014), pyrodiverse (Nimmo *et al.* 2019) landscapes with greater vegetation cover (Geary *et al.* 2018; Sukma *et al.* 2019).

Materials and methods

Study area

Our study was located in the Big Desert State Forest, Big Desert Wilderness Area, and Wyperfeld National Park (hereafter called the BDW complex), which cumulatively make up ~7000 km^2 of protected semi-arid mallee and heathland habitat in north-western Victoria on Wotjobaluk Country (Fig. 1). The BDW complex receives an annual average of ~350 mm of rain (Australian Bureau of Meteorology, http://www.bom.gov.au/), but with high variability influenced by El Niño/Southern Oscillation (ENSO) phases. The area received lower than average rainfall in 2021, with ~260 mm, but a much greater than average ~550 mm across 2022, during a strong La Niña ENSO phase (Australian Bureau of Meteorology).

Fire is an important driver in the BDW complex (Clarke *et al.* 2021), with large scale bushfires occurring at ~15-year intervals, and >2% of the BDW complex burned annually (Pausas and Bradstock 2007). The intense flammability of mallee and heath vegetation, combined with strong horizontal and vertical continuity in vegetation structure, has often resulted in bushfires spreading across a large extent of the park complex, resulting in homogeneity in the growth stages of recovering vegetation (Clarke *et al.* 2021).

Predator management has been conducted by management organisations within the BDW complex for at least the last 20 years (Robley and Choquenot 2002), although intermittent lethal control of dingoes (also known as 'Wilkerr' in Wergaia language) has been ongoing since early British colonisation of the area in the 1860–1870s (Alpin *et al.* 1987). Previously, baiting for foxes and dingoes was conducted yearly by Parks Victoria and the Victorian Department of Energy, Environment and Climate Change (DEECA) park management staff. Baiting was conducted through the deployment of 100–200 g cubes of boiled liver injected with aqueous 1080, with the concentration for fox baits deployed in Victoria 3 mg/bait, and 6 mg/bait for dingoes (APVMA 2008). Predator baiting in the BDW complex was performed to reduce the potential predation impact on vulnerable species such as the malleefowl (*Leipoa ocellata*) and livestock on neighbouring private properties. Fox baiting has been primarily conducted throughout the north of the BDW complex (Fig. 1). Dingo baiting was conducted within a three kilometre 'buffer zone' which extends from the public-private land interface and into the BDW complex (Fig. 1), under the Dingo Unprotection Order of Victoria's *Wildlife Act 1975* (S McLean, pers. comm. 2021), up until March 2024 when the Unprotection Order in this region ceased. Previously, both dingo and fox control were widely carried out on private property bordering the BDW complex, but this is no longer permitted for dingoes on private land as of March 2024.

Bait and camera deployment

To determine the rate of interaction of target and non-target species with liver baits deployed in the BDW complex, cameras were deployed to monitor buried baits. Monitoring of sand-pads for footprints and digging signs is commonly used to assess bait uptake (e.g. Allen *et al.* 1989; Dexter and Meek 1998; Thomson and Kok 2002), but there are examples where sand-pad monitoring has resulted in overestimations of the bait uptake rate by target species (Robley *et al.* 2009; Robley *et al.* 2011), and differences between bait take rates

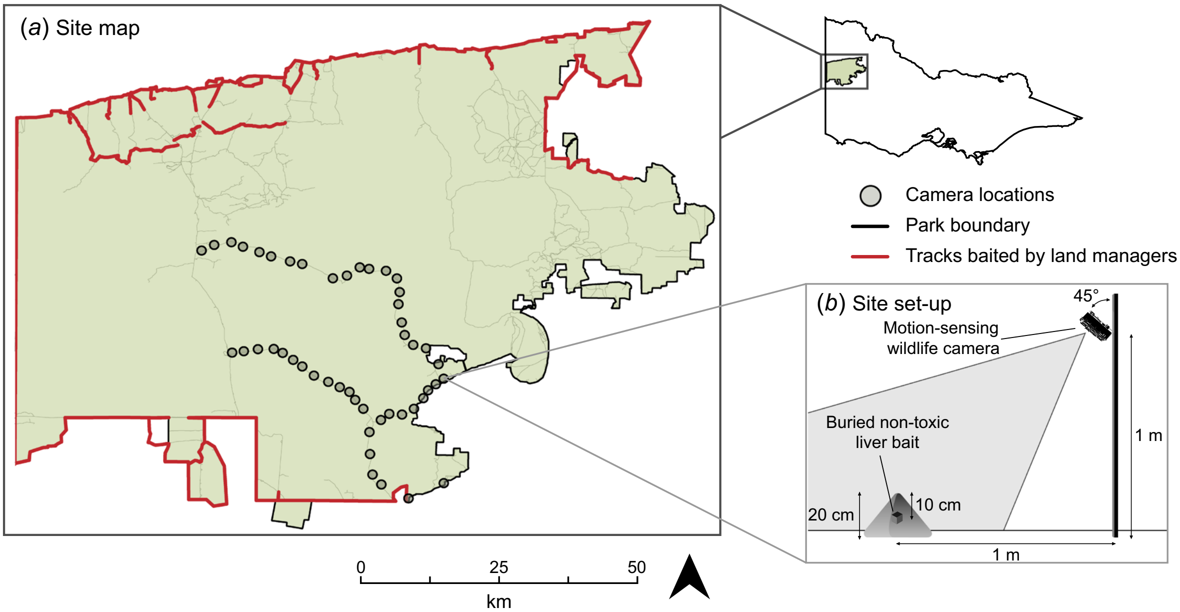

Fig. 1. (*a*) Locations of 48 cameras deployed within the Big Desert-Wyperfeld complex (south-eastern Australia) to monitor target and non-target species interactions with non-toxic liver baits. Camera and bait locations are denoted by circles. Areas marked with red indicate where lethal control with toxic 1080 baits has been conducted by land managers within the 5 years prior to this study. Tracks marked with black lines delineate public-private land boundaries where lethal control has not been conducted by land managers but may have been conducted by private landholders. Internal unbaited park tracks are marked with grey lines. (*b*) Set-up of wildlife camera and burial method of non-toxic liver bait at each camera deployment site.

reported by sand-pad monitoring and cameras (Glen and Dickman 2003*b*; Robley *et al.* 2011; Kreplins *et al.* 2018). Additionally, wet weather and extensive digging by foxes are known to obscure signs of other species at bait stations (Belcher 1998; Fairbridge *et al.* 2000; Glen *et al.* 2007). Hence, to ensure accurate identification of species at bait sites, motion activated wildlife cameras were used in our study.

A total of 48 sites were selected along a gradient from the boundary to the interior of the BDW complex, which is correlated with distance from areas where lethal baits had been deployed in the 5 years prior to our study (Fig. 1). Sites were a minimum of 1.5 km apart and 50 m (±10 m) adjacent to tracks in vegetated areas. Baits were deployed to mirror 'best practice' methods for reducing non-target uptake in Victoria – non-toxic Foxoff™ free-feed cooked liver baits (Animal Control Technologies Pty Ltd), which had been dyed blue, were buried to a depth of 10 cm into a mound of sand 20 cm high in mid-late autumn (Fig. 1). This aligned with the timing and methodology of lethal predator control conducted annually in the BDW complex by DEECA (S McLean, pers. comm. 2021). Immediately adjacent to the buried liver baits, one metre from the centre of the sand mound, a Swift Enduro wildlife monitoring camera was attached to a wooden stake one metre above the ground. Cameras were mounted facing south, to minimise solar glare, at a 45-degree angle with the sand mound at the centre of the camera field of view (Fig. 1). Camera sensitivity was set to high, with no quiet period between triggers, and five images were captured one second apart for every trigger. Cameras were deployed at the same time baits were buried and were retrieved 70 days later. This deployment length was selected to capture the entire period over which buried lethal baits likely retain a 1080 dose higher than the median lethal dose (LD_{50}) for an adult fox under typical environmental conditions (Saunders *et al.* 2000; Allsop *et al.* 2017). All cameras were still functioning when retrieved.

Image labelling

A total of 36,129 images were captured over 3360 camera trap nights. Images were imported into open-source image-labelling program Camelot (Hendry and Mann 2018). Animals detected in camera images were identified to species-level wherever possible, and two behaviours were classified: 'digging', where a species was actively digging into the centre of the mound of sand containing the buried liver; and 'eating', where species were seen to be consuming some or all of the bait.

Digging and eating behaviours of small mammal species were difficult to differentiate accurately and consistently, particularly in infrared images taken at night, so consequently 'digging' and 'eating' behaviours were grouped and collectively labelled as 'bait interactions'. This allowed us to investigate instances where species directly consumed baits, but also instances where species contributed to making a buried bait available (exposing it or bringing it to the sand surface) for potential consumption by other animals. Detections and bait interactions were defined as independent when there was greater than 20 min between successive images of the same species at a site. This independence threshold accommodated species that were more likely to linger in front of cameras for extended periods, such as large herbivores, but reduced the likelihood of incorrectly filtering out valid observations of smaller, fast-moving species such as rodents (Rendall *et al.* 2014; Meek *et al.* 2014; Iannarilli *et al.* 2021).

Environmental variables

Five environmental variables were measured across the BDW complex to investigate variation in species' interactions with baits: park boundary distance, vegetation cover, fire frequency, pyrodiversity, and time since fire. Variables were either measured as straight-line distance (park boundary distance) or calculated within a 750 m radius around each camera location (vegetation cover, fire frequency, pyrodiversity, and time since fire). This buffer was chosen to capture contrast in environmental variables over a meaningful area for both larger and wide-ranging species (e.g. dingoes, foxes and kangaroos) and more range-restricted species (e.g. rodents; Nimmo *et al.* 2019). Buffers around sites that bordered agricultural land excluded farmland from the calculations of environmental variable values. As we were measuring bait interactions within a remnant semi-arid mallee ecosystem, environmental conditions in adjacent farmland were excluded as not reflective of conditions inside the park.

Park boundary distance

To capture variation in species' response based on distance to adjacent farmland (i.e. 'edge effects'; Yahner 1988; May and Norton 1996), a measure of the straight-line distance in metres from the bait deployment location to the nearest boundary of the park complex was recorded for each site.

Vegetation Cover

Vegetation cover was determined with a rasterised layer containing overlapping projected foliage cover of indigenous plant lifeforms occurring within the study system, including all native species of trees, shrubs, chenopods, tussock grasses, hummock grasses, and forbs (M White, pers. comm. 2024). This vegetation cover layer was generated from a subset of plant lifeform distributions mapped as part of a separate project (M White, pers. comm. 2024), where weighted modelling of more than 57,000 field measured vegetation plots resulted in spatial models of 'benchmark' ('pre–1750') lifeform cover across south-eastern Australia. Percent cover of the perennial life-form types occurring in Victorian mallee dune field ecosystems were summed to generate a total vegetation cover score and clipped by the extent of remnant native vegetation landcover (to account for areas which have been cleared for agriculture or infrastructure post–1750). As mallee ecosystems are generally sparsely vegetated, cover scores for 40 × 40 metre grid cells ranged from ~10% to 29%. Mean vegetation cover was calculated across buffers surrounding each site.

Fire history

Three fire history variables were calculated across site buffers. All fire history variables included both planned burns and bushfires, as most fires in mallee ecosystems are stand-replacing (Haslem *et al.* 2011) and as such, there is similar fire intensity and ecosystem outcomes for both. All fires in the recorded history of the BDW complex between 1930 and March 2022 were included in the analysis. The three variables included: fire frequency, pyrodiversity, and time since fire. Fire frequency represented the number of times each site had previously burned. 40 × 40 metre grid cells across the entire park were assigned a value based on the number of burns overlapping each cell, and the mean frequency of burns was calculated for each site. Pyrodiversity represented the variation in fire frequency surrounding each site. Previous research, including within the same study system (Geary *et al.* 2018), has identified that variability in fire age classes within a defined area (i.e. 'pyrodiversity') can be beneficial to and increase the abundance of some species, particularly species that benefit from variation in the level of vegetation cover (e.g. silky mice (*Pseudomys apodemoides*) in the BDW complex; see Geary *et al.* 2018). The pyrodiversity score for each site was generated by taking the standard deviation of fire frequency. Time since fire represented the proportion of each site that was recently burned (fire < 11 years ago), of a mid-successional fire age (fire 11–35 years ago), and long-unburned (fire > 35 years ago; fire intervals adapted from Geary *et al.* 2018). To reduce potential correlation in predictor variables, a Principal Component Analysis (PCA) was conducted on the three proportions. Two Principal Components (PCs) that explained 100% of the variance in the three categories were generated (Fig. S1). The first component (hereafter *'mid to late successional'* PC; *Eigenvalue* = 1.95) represented a gradient from mid-successional time since fire (low values) to areas that are long-unburned (high values). The second component (hereafter 'recently burned' PC; *Eigenvalue* = 1.05) described a gradient from recently burned areas (low values) to areas associated with either mid-successional or long-unburned fire ages (high values). PC scores were approximately equally weighted across the original recently burned, mid-successional, and long-unburned categories (Fig. S1).

Statistical approach and analysis

Species detections and bait interactions

To determine whether the number of detections of each species was proportional to the number of bait interactions, and whether this detection–bait interaction ratio differed between target and non-target species, detections and bait interactions by all species that recorded bait interactions (excluding unidentifiable animals) were separately totalled.

The relative proportion of total detections and bait interactions attributable to each species was then calculated.

Timing of bait interactions by species

To quantify whether target species found and interacted with baits more quickly than non-target species, we compared the time taken for the first bait interaction by each species at a site. First bait interaction events by species at sites were blocked into five 14-day periods: 0–14 days post deployment, 15–28 days, 29–42 days, 43–56 days, and 57–70 days. A Chi-square Test of Independence with Markov Chain Monte Carlo simulation was run to compare the likelihood of a species interacting with a bait within each of the five two-week blocks. Standardised residuals with the greatest magnitude difference from the mean (±2 in this study) were identified as strong contributors and reported accordingly.

Impact of environmental variables on bait interactions

The impact of environmental variables on the likelihood of species to interact with baits was investigated through two pathways: with an all-species model, including every species who had recorded at least one bait interaction, and with individual species models, for species with sufficient detections and bait interactions to model independently. For all models, environmental variables were scaled and centred (except PC scores). Correlation between all covariates was tested and variables with a correlation coefficient > 0.7 were inspected (Fig. S2). Fire frequency and *mid to late successional* PC were negatively correlated ($r_p = -0.79$; Fig. S2). As time since fire is a key predictor of community composition in this ecosystem, and there is less understood about the effects of fire frequency on animal populations (Clarke *et al.* 2021), we excluded fire frequency from further analysis. All remaining covariates had correlation coefficients < 0.4 (Fig. S2).

There were no *a priori* expectations for the impact of each environmental variable on the likelihood of target and non-target species interacting with baits. For the all-species model, initial global generalised linear mixed effects models (GLMMs) included all uncorrelated environmental variables and their interaction with 'target' versus 'non-target' species (a two-level categorical variable). Site was included as a random effect to account for instances where multiple species were detected or interacted with a bait at the same site. For individual species models, initial global generalised linear models (GLMs) included all uncorrelated environmental variables. Due to sample size constraints, we limited the number of covariate combinations in model selection in the all-species model to six, and for individual species models to four, to reduce potential overparameterization.

The all-species model and individual species models were run with a binomial distribution to avoid issues with potential non-independence of detections or bait interactions (including individual sites with many bait interactions by single species). Global models were validated to ensure model assumptions were met with diagnostic plots. Residuals vs Leverage was graphed to identify the presence of any significant outliers (defined as having a cook's *D* statistic >1). Global models with identified outliers were tested with and without the outliers present to determine their impact on overall result, and where overall trends did change, results with and without the outlier are reported. Resulting models were ranked using Akaike Information Criterion with correction for small sample sizes (AIC_C) and AIC_C weights (ω_i). All models with $\Delta AIC_C > 2$, or models ranked below the null model, were not considered further. Where there was model selection uncertainty, covariates that appeared in all models with a delta AIC < 2 are reported. The confidence level for result reporting was selected at 85% confidence intervals (CI) to reduce the likelihood of including uninformative parameters in result interpretations (Arnold 2010; Leroux 2019).

Animal ethics

Study methods were approved by Deakin University's Animal Ethics Committee Wildlife-Burwood (AECW-B Permit number B07-2021), and Parks Victoria (Access Agreement Permit: 'Assessing fox, dingo, and wild dog management, and its ecosystem consequences, in semi-arid Victoria').

Results

Detections and bait interactions

A total of 716 independent observations of animals were recorded on cameras at bait sites (Supplementary material; Table S1). This included 558 mammal detections from 12 identified species, with the most common being Mitchell's hopping-mice (*Notomys mitchellii*; 20% of observations), silky mice (16%), European rabbit (9%) and western grey kangaroo (*Macropus fuliginosus*; 8%) (Table S1). Birds were detected 127 times across 18 species, with chestnut quail-thrush (*Cinclosoma castanotum*; 4%), grey shrike-thrush (*Colluricincla harmonica*; 3%) and pied currawong (*Strepera graculina*; 2%) detected most often (Table S1). Reptiles from three species groups were detected 25 times, including painted dragons (*Ctenophorus pictus*; 1%) and central bearded dragons (*Pogona vitticeps*; <1%) (Table S1). Six detections were not able to be assigned to a species group (Table S1).

A total of 145 bait interactions were recorded for nine mammal species (Table S1). No birds or reptiles were recorded interacting with baits, they were only recorded passing through the camera area or perching/basking on the sand mound, without exhibiting any digging behaviour.

Both target species – foxes and dingoes – were detected at bait sites and interacted with baits. Foxes were observed at 17 sites (35%), and 32 bait interactions were recorded across 14 sites (Table 1). Dingoes were detected once with a single

Table 1. Mammal species recorded interacting with non-toxic liver baits in the Big Desert-Wyperfeld complex, south-eastern Australia.

Species	Sites detected	Sites with bait interactions	Detected sites with bait interactions (%)
Mitchell's hopping-mouse (*Notomys mitchellii*)	26	16	61.5
Silky mouse (*Pseudomys apodemoides*)	24	7	29.2
Western grey kangaroo (*Macropus fuliginosus*)	20	6	30.0
Fox (*Vulpes vulpes*)	17	14	82.4
House mouse (*Mus musculus*)	13	6	46.2
European rabbit (*Oryctolagus cuniculus*)	8	3	37.5
European hare (*Lepus europaeus*)	4	2	50.0
Short-beaked echidna (*Tachyglossus aculeatus*)	4	2	50.0
Dingo (*Canis dingo*)	1	1	100.0

detection and bait interaction at only one site (2%) (Table 1). Dingoes are known to occur in the area surrounding the locations of these cameras and have previously been detected within 3.5 km of multiple bait sites (R.T. Mason, unpubl. data).

Seven non-target mammal species were detected at bait sites and were recorded interacting with baits. Mitchell's hopping-mice were recorded at the highest number of camera sites (54% of sites) and interacted with baits at the most sites (33%; Table 1). In total, Mitchell's hopping-mice were detected 146 times, and recorded 43 bait interactions. Silky mice were also frequently detected (n = 116 detections) at a high number of sites (n = 50% of sites; Table 1). Silky mice recorded the highest number of bait interactions of any species (n = 54 bait interactions), but this was constrained to a small number of sites (n = 15%), with 46 of these bait interactions happening at a single site. Three mammal species that were detected on cameras were not recorded interacting with buried bait mounds: feral cats (*Felis catus*, n = 7 detections), common dunnarts (*Sminthopsis murina*, n = 4 detections) and swamp wallabies (*Wallabia bicolor*, n = 1 detection).

Digging and eating behaviours could not always be accurately differentiated from camera images, however four mammal species were recorded partially consuming baits on camera on at least one occasion: foxes, western grey kangaroos, silky mice, and Mitchell's hopping-mice.

Target species accounted for more recorded bait interactions relative to their detection numbers, and when detected, were more likely to interact with baits compared to non-target species. Target species, primarily foxes, accounted for 7% of all species detections and 12% of all bait interactions, with only a single detection and bait interaction recorded by dingoes (Fig. 2). The seven non-target species that recorded bait interactions accounted for 93% of detection records and 88% of bait interactions. Two non-target species, silky mice and short-beaked echidnas (*Tachyglossus aculeatus*), frequently interacted with baits when detected at sites and consequently accounted for a greater proportion of bait interactions relative to their detection rate. The five remaining non-target species had fewer bait interactions relative to the number of times they were detected (Fig. 2).

Timing of bait interactions by species

There was a significant difference in the time taken for each species to first interact with baits (χ^2 = 50.52, P = 0.011). Foxes and dingoes took the greatest number of days to first interact with buried baits (median time to first bait interaction, foxes: 42 days, dingoes: 60 days). A single fox interacted with a buried bait within 14 h of bait deployment, but the next interaction was after 19 days (Fig. 3). There were significantly fewer bait interactions in the 0–14-day period than expected (χ^2 standardised residual = −2.78; Fig. 3). Bait interactions by foxes were greater than expected 42–56 days after deployment (χ^2 standardised residual = 2.69; Fig. 3). The single dingo that recorded a bait interaction did so after 60 days, which was greater than expected for the 56–72-day period (χ^2 standardised residual = 2.50; Fig. 3).

Three non-target species had greater than expected bait interactions at different periods in the bait deployment. Mitchell's hopping-mice had a higher-than-expected number of bait interactions in the 0–14-day period (χ^2 standardised residual = 2.32; Fig. 3), interacting with baits at ten sites in the first 6 days. Within the 14–28-day period, there were greater than expected bait interactions by silky mice (χ^2 standardised residual = 2.31; Fig. 3). Comparatively, western grey kangaroos bait interactions were greater than expected in the last period, 56–72 days after bait deployment (χ^2 standardised residual = 2.68; Fig. 3).

Impact of environmental variables on bait interactions

All-species model

A total of 117 records from the nine mammal species that interacted with baits were included in this analysis, with a minimum of one record from each camera site. 18 records were from target species (overwhelmingly represented by foxes; n = 17) and 99 records were from non-target species.

There was some model selection uncertainty. The best-supported model included pyrodiversity, the *mid to late successional* PC, and species (target/non-target) status (AIC_C ω_i = 0.044). Additional variables were supported in models with $\Delta AIC_C < 2$, but these variables all met the criteria for uninformative parameters (Leroux 2019; Table S2) and were,

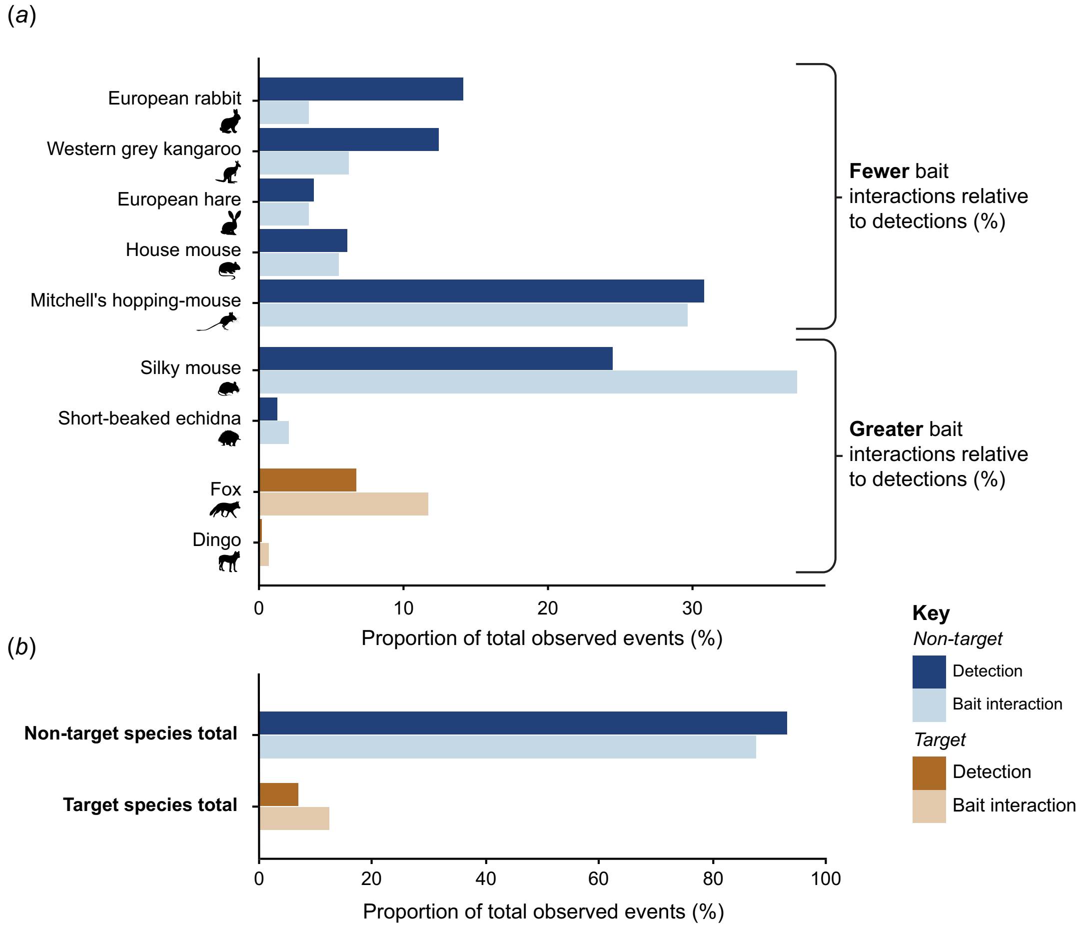

Fig. 2. Clustered bar chart depicting the percentage of detections (darker coloured bars) and bait interactions (lighter coloured bars) by (*a*) each target (orange) and non-target (blue) species and (*b*) all target and non-target species combined. A temporal filter of 20 min between successive images of a species was used to determine independence of detections (n = 474 detections) and bait interactions (n = 145 bait interactions). Bait interactions were defined as records of an identifiable species actively digging into a buried bait sand mound or otherwise interacting with the bait. Detections of species which did not record bait interactions (n = 170) and detections and bait interactions by unidentifiable mammals (n = 72 detections, 1 bait interaction), have not been included in this figure.

therefore, not interpreted further. Target species, primarily represented by foxes, were twice as likely (83%) to interact with baits (estimated marginal means (EMM) = 0.83, 85% CI = 0.66 to 0.93) when compared to non-target species (42%; EMM = 0.42, 85% CI = 0.35 to 0.50). Bait interactions were more likely to be recorded at sites with greater pyrodiversity across the surrounding landscape (β = 1.43, 85% CI = 0.24 to 2.63). There were also more bait interactions at sites with a higher proportion of mid-successional time since fire and a lower proportion of long-unburned areas (β = –0.24, 85% CI = –0.45 to –0.03).

Individual species models

Four mammal species were detected at more than 15 sites, allowing for further investigation into variables that may be driving responses in each species: foxes (n = 17 sites; Table 1), western grey kangaroos (n = 20 sites; Table 1), Mitchell's hopping-mice (n = 26 sites; Table 1) and silky mice (n = 24 sites; Table 1).

The best-supported model for the bait interaction response of foxes (Table S3) included park boundary distance and vegetation cover (AICc ω_i = 0.085). There were no additional supported variables in models ranked above the null model (ΔAICc = 0.27). Greater distance from park boundaries (β = 3.44, 85% CI = –0.62 to 7.49) and increased vegetation cover (β = 13.98, 85% CI = –1.93 to 28.891) generally increased the likelihood for foxes to record bait interactions, however confidence intervals for both coefficients overlapped zero (Fig. 4).

The bait interaction response of western grey kangaroos was influenced by an outlier (Cook's D = 1.20) that altered the overall result trends when the global model was tested

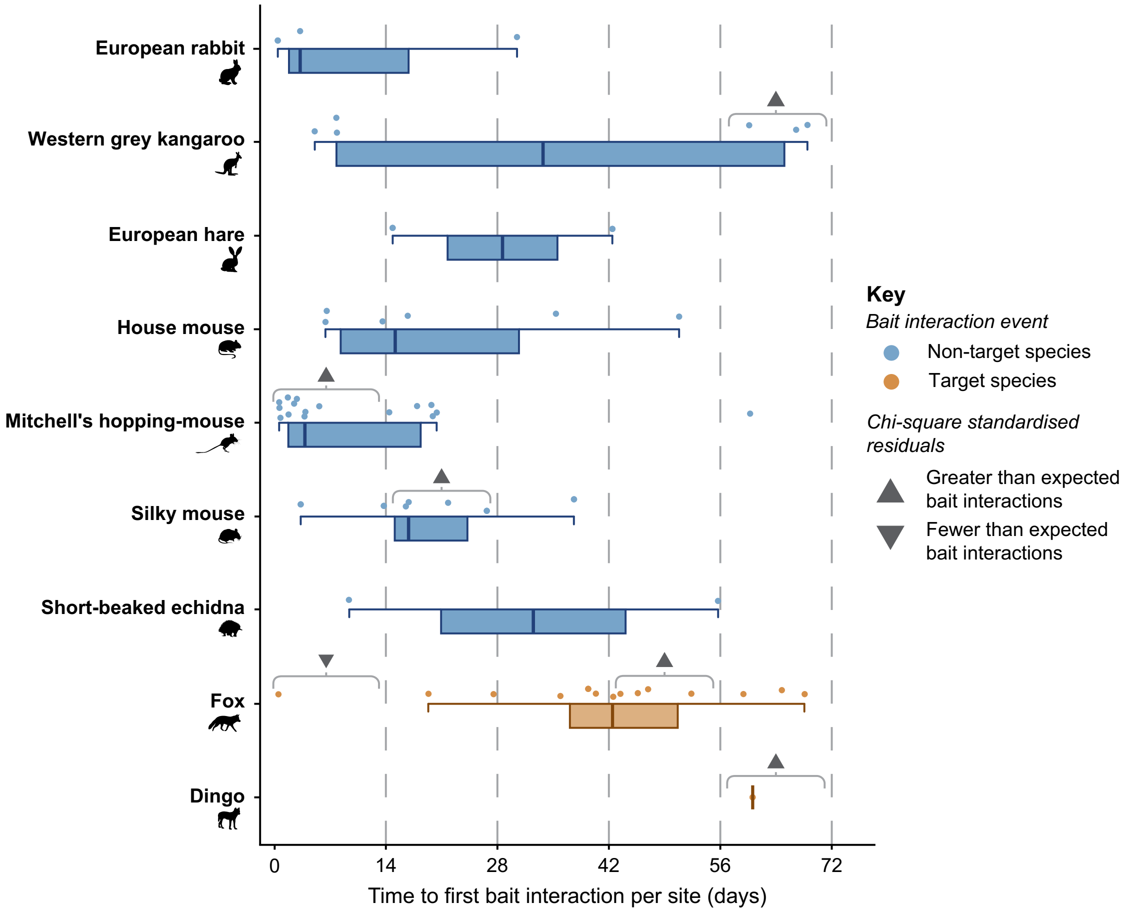

Fig. 3. Box plot and dot plot depicting the time taken (in days) to record the first bait interaction by non-target (blue) and target (orange) species at camera sites in the Big Desert-Wyperfeld complex. Thick lines indicate median time for each species, boxes show the interquartile range (IQR), and whiskers depict 1.5 × IQR. Grey arrows correspond to significant results of a Chi-square with Markov Chain Monte Carlo simulation ($\chi^2 = 50.52$, $P = 0.018$). Up arrows indicate standardised residuals with a strong positive magnitude (>2), denoting periods where a species interacted with baits more than expected, and down arrows indicate a strong negative magnitude (<−2), denoting periods where species interacted with baits less than expected.

with and without its inclusion (Table S3). With the outlier included, the best-fit model for western grey kangaroos was the null model (AIC_C $\omega_i = 0.214$; Table S3). With the outlier removed, the only model that ranked above the null model (ΔAICc = 1.07) included the park boundary distance and *recently burned* PC as covariates (AIC_C $\omega_i = 0.217$, Table S3). When the outlier was not considered, the likelihood of western grey kangaroos to interact with baits increased with park boundary distance ($\beta = 4.23$, 85% CI = 1.42 to 8.27), and with a higher proportion of recently burned areas ($\beta = -1.19$, 85% CI = −2.31 to −0.35). As the sample size was constrained in the single species models, outliers could have strong impacts on overall model outcomes. Results excluding the outlier should be interpreted in a cautionary manner.

There was model selection uncertainty for Mitchell's hopping-mice, as the top two models had equal weight (AIC_c $\omega_i = 0.132$; Table S3). The top supported model included pyrodiversity, and the second-best model was the null model. As such, while there is an apparent trend towards Mitchell's hopping-mice being more likely to interact with bait mounds at camera sites with more variation in the fire age of the surrounding vegetation ($\beta = 1.68$, 85% CI = 0.10 to 3.49; Fig. 4), this result should be interpreted with caution.

Silky mice models indicated strong support for pyrodiversity and the *mid to late successional* PC. All other variables (vegetation cover and park boundary distance) met the criteria for uninformative parameters and were not interpreted further (Leroux 2019; Table S3). Silky mice were more likely to interact with baits at camera sites with a higher diversity of fire age in the surrounding landscape ($\beta = 5.74$, 85% CI = 1.94 to 10.87; Fig. 4), and with a greater proportion of mid-successional time since fire relative to the proportion of long-unburned areas ($\beta = -0.91$, 85% CI = −1.73 to −0.28; Fig. 4).

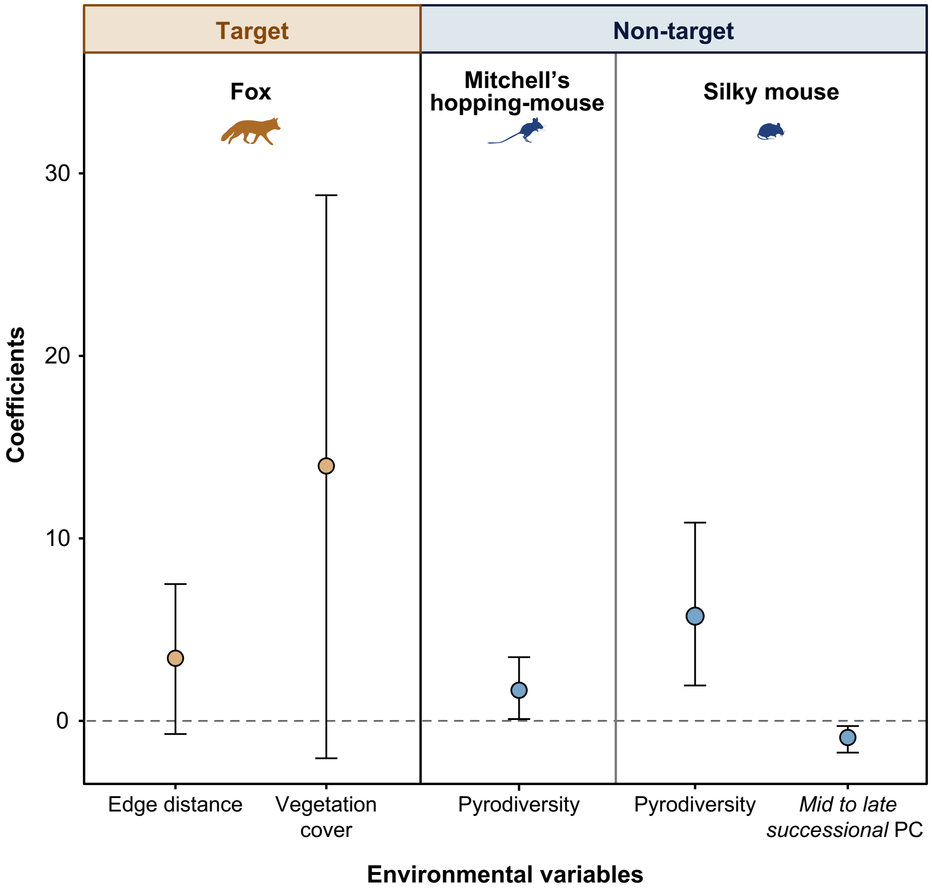

Fig. 4. Forest plot depicting the influence of environmental variables on the likelihood of species interacting with buried meat baits at camera sites in the Big Desert-Wyperfeld complex. Estimates ± 85% confidence intervals for variables included in the best-fit binary generalised linear model (GLM) outputs for target species (orange; foxes (*Vulpes vulpes*), $n = 17$ sites) and non-target species (blue; Mitchell's hopping-mice (*Notomys mitchellii*), $n = 26$ sites; and silky mice (*Pseudomys apodemoides*), $n = 24$ sites) are shown. Confidence interval brackets that do not overlap zero (dashed grey line) are considered significant.

Discussion

Understanding how target and non-target species may be impacted by lethal predator control is essential for achieving management goals and to limit any unintended negative consequences. In our study, using baiting methods recommended to reduce non-target bait interactions, we found that both target species, foxes and dingoes, interacted with buried non-toxic baits. However, they were typically not the first nor the most common species to interact with baits. Instead, native non-target species, particularly Mitchell's hopping-mice and silky mice, were more likely to dig up or consume baits, and in a shorter timeframe than target predator species. The likelihood of non-target species interacting with buried baits was impacted by environmental variables including pyrodiversity, time since fire and vegetation cover. Our results reveal that lethal control programs have the potential to impact communities and hence ecosystems in unexpected ways.

Target and non-target bait interactions

Target species for lethal predator control – foxes and dingoes – did not detect and interact with buried baits more frequently than non-target species did. The proportion of bait interactions by target species recorded in this study is low in comparison to previously reported bait uptake rates for foxes and dingoes (i.e. bait uptake between <1% and 35% for similar deployment methods: Thompson and Fleming 1994; Saunders *et al.* 1999; Glen and Dickman 2003*a*; Dundas *et al.* 2014). Despite implementing 'best practice' methods for reducing non-target bait interactions, non-target species accounted for ~90% of bait interactions, nearly two-thirds of which were by Mitchell's hopping-mice and silky mice. Bait uptake rates by native rodent species have rarely been quantified, although Moseby *et al.* (2011) detected spinifex hopping mouse (*Notomys alexis*) and greater stick-nest rats (*Leporillus conditor*) partially consuming surface-laid baits at 16% of bait stations.

Contrary to our predictions, all non-target species generally interacted with baits earlier in the deployment period than either foxes or dingoes. The single dingo and the majority of fox bait interactions occurred late in the bait deployment period. Due to rapid degradation of 1080 in wet conditions (Saunders *et al.* 2000; Allsop *et al.* 2017), the greater than average rainfall occurring throughout this experiment likely meant that if toxic baits had been used, only three target animals may have ingested a lethal or sublethal 1080 dosage. Despite the lower numbers and slower time for bait interactions by target species, in cases where they were detected at camera sites, foxes and dingoes were twice as likely to interact with baits than non-target species were. This suggests that target species may be more intentional in digging up and consuming buried baits, whereas non-target animals, including herbivorous or granivorous species, are potentially opportunistically digging up baits for the abundant and easily accessible source of protein.

Impact of environmental variables on bait interactions

When evaluating all nine species' response to baiting, bait interactions were more likely to occur in areas with increased pyrodiversity and a greater proportion of mid-successional vegetation, compared to long-unburned areas. Individually, greater pyrodiversity also increased the likelihood of bait interactions by Mitchell's hopping-mice, and both pyrodiversity and mid-successional vegetation were associated with increased bait interactions by silky mice. Many vegetation attributes that influence habitat suitability in mallee environments are strongly influenced by time since fire and pyrodiversity (Haslem *et al.* 2011; Kelly *et al.* 2012). Understory and midstory complexity peak in mid-successional time since fire areas (Haslem *et al.* 2011), and these densely vegetated microhabitats can provide important shelter resources to aid predator avoidance (Di Stefano *et al.* 2011). Previous research has shown that more open microhabitats in recently burned areas reduce the foraging time of Mitchell's hopping-mice and other rodent species, compared to foraging in sheltered shrub-covered microhabitats (Doherty *et al.* 2015). Digging up and consuming baits in a cleared, bare ground area results in lengthy periods of exposure for small prey species. Access to nearby unburned mid-successional vegetation in pyrodiverse landscapes can provide rapid shelter from approaching predators (Doherty *et al.* 2022), explaining the influence of these factors on bait interaction rates by native mice in this study.

Foxes interacted with baits at >80% of sites where they were detected. Foxes are an opportunistic, generalist species with a broad diet (Fleming *et al.* 2021), meaning they're predisposed to interacting with baits. In this study, contrary to predictions, greater distance from the park boundary and increased vegetation cover were associated with an increased likelihood of bait interactions by foxes. Lethal baiting in the BDW complex is concentrated on the northern and southern boundaries, potentially reducing the likelihood of foxes consuming baits at park edges due to selection pressure (Allsop *et al.* 2017) and/or a localised reduction in fox abundance after previous baiting (Carter and Luck 2013). Additionally, human-modified or fragmented landscapes including farmland and open habitat edges can be associated with greater prey density (Šálek *et al.* 2010), prey vulnerability (Panzacchi *et al.* 2009; Doherty *et al.* 2022) and anthropogenic food resources (Hradsky *et al.* 2017*b*). Foxes with home ranges in the continuous, highly vegetated interior of the park complex may be more likely to interact with baits due to differences in resource availability associated with these complex habitats. Future research should focus on clarifying potential differences in the response of foxes to baiting in intact and fragmented landscapes, and in relation to prey availability.

Bait interactions by western grey kangaroos tended to increase with distance from the edge of the park complex and in recently burned areas, but these trends were only apparent in models where an outlier was removed. When considered in association with the small sample size, these trends should be interpreted cautiously. Western grey kangaroos preferentially feed on grasses (Arnold *et al.* 1989), including pasture and crops around the BDW complex (Short and Grigg 1982), and the sclerophyllous shrub understory of denser mallee habitats may not provide nutrient-dense food resources (Short and Grigg 1982). As such, with increasing distance from the edge of the BDW complex, western grey kangaroos may be attracted to recently burned areas due to highly palatable reshooting vegetation and may be consuming meat baits as a source of protein. Previous published occurrences of western grey kangaroos scavenging carrion or consuming meat baits have all been in sandy, nutrient poor environments (Dundas *et al.* 2014; Hughes and Bérengier 2018), comparable to the conditions in this study.

Factors affecting efficacy of baiting programs

The low numbers and slow time frame of target species interacting with baits could be influenced by climatic conditions during this period. This study was undertaken during a period of above average rainfall (Australian Bureau of Meteorology). Increases in native small mammal populations have been linked to increased rainfall in the previous 6–12 months (Letnic and Dickman 2006; Kelly *et al.* 2012; Christensen *et al.* 2013; Bennison *et al.* 2018). Similarly, rabbit and kangaroo abundance can increase following rainfall events in arid and semi-arid environments (Wood 1980; Caughley *et al.* 1984; Cairns and Grigg 1993). These species collectively make up a high proportion of the diet of both foxes and dingoes in this park complex (Ritchie 2013; Davis *et al.* 2015), so increased prey abundance could be reducing the scavenging of buried baits by these species.

Dietary switching with changing availability of prey species is well-demonstrated in dingoes and foxes (Doherty *et al.* 2019; Fleming *et al.* 2021) and scavenging rates can vary in response to fluctuating live prey abundance (Allen 2010; Forsyth *et al.* 2014). However, the direct influence of prey availability on bait uptake has thus far only been demonstrated in cats, with increasing rabbit (Algar *et al.* 2007) and small mammal (Christensen *et al.* 2013) abundance shown to substantially reduce bait uptake in semi-arid areas, and conversely, nutritional stress increasing records of bait scavenging by cats in arid areas (Paltridge *et al.* 1997).

This inverse relationship between prey abundance and bait scavenging rates could also explain the lack of bait interactions recorded by cats, varanids, and corvids in this study, as varanids (Moseby *et al.* 2011; Kreplins *et al.* 2018) and corvids (Dexter and Meek 1998; Kreplins *et al.* 2018; Hohnen *et al.* 2020) are frequently responsible for non-target bait uptake in monitored baiting trials, but did not interact with baits in our study.

Conservation and management implications

Lethal control with 1080 is a widespread method of predator management in Australia and New Zealand, and can be an effective conservation tool (e.g. Morris *et al.* 2003; Dexter and Murray 2009; Kinnear *et al.* 2010; Kirkwood *et al.* 2014; Robley *et al.* 2014; Nichols *et al.* 2021). However, the impacts of 1080 baiting on non-target species, including when 'best practice' baiting techniques are used, are often unquantified (Glen *et al.* 2007). Here, we have reported that bait burial to 10 cm, reduced bait palatability, and targeted timing of bait deployment did not subsequently result in a lack of non-target bait interactions. The low level of bait interactions recorded by foxes and dingoes in this study, and high levels recorded by native non-target animals, imply that poison baiting may be less effective at controlling predators in this region than expected. Our study has also identified a relationship between increased non-target bait interactions and fire history variables, which is often overlooked in the design of lethal predator control programs. Baiting programs that do not consider the influence of fire history on non-target bait interactions may deploy baits in areas where non-target species are more likely to dig up and consume them, and target species are less likely to. This will not only reduce the efficacy for target species, but may also harm non-target populations.

There are two possible outcomes of non-target species digging up baits, both of which have implications for conservation and management outcomes of lethal control programs. The first is that a non-target animal consumes the bait, and the alternative is that the bait becomes available in the environment after a non-target animal digs it up but does not consume it.

Bait consumption by non-target species

The consequence of consumption of some or all of a lethal bait by a non-target animal will vary based on the sensitivity and susceptibility of that species to 1080 ingestion. Some native mammals are reported to be highly tolerant to 1080, especially if their distribution overlaps vegetation with high levels of naturally occurring fluoroacetate (reviewed in Twigg and King 1991). Western grey kangaroos, for example, have demonstrated a high tolerance (LD_{50} 20–60 mg kg^{-1}; Mcilroy 1982*a*) for 1080 across their entire distribution (Oliver *et al.* 1979), and are unlikely to be affected even by consumption of multiple toxic baits. However, some species have demonstrated reduced 1080 tolerance in populations with increasing geographic separation from fluoroacetate-rich plants (Calver *et al.* 1989; Twigg *et al.* 2003). Mitchell's hopping-mouse populations range from an LD_{50} of 51 mg kg^{-1} (Twigg *et al.* 2003), to 14 mg kg^{-1} (Calver *et al.* 1989) with increasing distance from naturally occurring fluoroacetate. Mitchell's hopping-mice in the BDW complex, at the eastern-most extent of their distribution, may have a much lower tolerance than previously tested populations. The sensitivity of silky mice to 1080 poison has never been experimentally tested, but adult silky mice in the BDW complex have been reported dying after exposure to 1080-poisoned oat baits (Cockburn 1981; Mcilroy 1982*b*). Populations of the most closely related species, the ash-grey mouse (*Pseudomys albocinereus*) that do not overlap with fluoroacetate-rich plants, are highly sensitive to 1080, with an LD_{50} of 1.57 mg kg^{-1} (Twigg *et al.* 2003). Silky mice, with no evolutionary exposure to fluoroacetate, would likely be equally or more sensitive to 1080.

To consume a potentially lethal 1080 dose, adult Mitchell's hopping-mice, weighing ~52 grams (Menkhorst 2011) and assuming an LD_{50} of 14 mg kg^{-1}, would need to consume ~25% of a fox bait or 12% of a dingo bait (containing 3 mg and 6 mg of 1080, respectively). Mitchell's hopping-mice have been recorded consuming up to eight grams of food daily (Calver *et al.* 1991) and could therefore consume a lethal or sublethal 1080 dose of dingo or fox bait in a single day. Similar estimates cannot be directly made for silky mice, but if they are as sensitive as the closely related ash-grey mice, a silky mouse weighing 22 grams would need to consume just 0.3 grams of meat from a 60-gram dingo bait to receive a potentially lethal 1080 dose. While some rodent species have been shown to reduce their consumption of 1080 injected food items (Calver *et al.* 1989; O'Connor *et al.* 2005), neither of these native species has previously demonstrated 1080 avoidance in lab or field settings (Cockburn 1981; Mcilroy 1982*b*; Calver *et al.* 1989). As we have recorded both species readily locating, digging up, and gnawing buried non-toxic baits deployed in the field, we can assume that both Mitchell's hopping-mice and silky mice are at risk of sublethal or lethal impacts of 1080 baiting programs conducted in this environment.

Increased bait availability. Even when not directly consuming baits, non-target species digging up baits will increase their availability to other species. Unburied baits are taken more often by corvids (Allen *et al.* 1989; Thomson and Kok 2002; Moseby *et al.* 2011), raptors (Moseby *et al.* 2011), varanids (Allen *et al.* 1989; Thomson and Kok 2002), and dasyurids (Mooney *et al.* 2005) than buried baits. Particularly concerning is the risk of increased bait availability to vulnerable dasyurids present in this study area, the fat-tailed dunnart (*Sminthopsis crassicaudata*) and the common dunnart (*Sminthopsis murina*). While dunnart species including fat-tailed dunnarts are generally considered highly sensitive to 1080 (Mcilroy 1981), common dunnart susceptibility has not been experimentally tested. Bait excavation by other non-target animals has the potential to impact these vulnerable species.

Conclusions

In the BDW complex, we have shown that ongoing landscape-scale baiting using 'best practice' baiting methods has the potential to negatively impact non-target native animals. More research into both the uptake of baits by non-target species, particularly native rodents, and the relationship between environmental variables and baiting in both target and non-target species, is needed across a variety of Australian landscapes to quantify the scope and severity of this problem. Simultaneously, efforts to monitor and reduce any non-target uptake of baits need to be considered and implemented where appropriate. Future research should also focus on quantifying the susceptibility of populations of non-target species across a range of geographic and ecological contexts. If the use of predator baiting as a conservation tool is to continue, it needs to be targeted, efficient and beneficial to the ecosystem. In the BDW complex, deploying baits as a direct response to conditions that will result in greater target uptake and reduced non-target interactions, such as immediately post-fire and in periods of low prey availability (Allen 2010; Forsyth *et al.* 2014), will both increase the efficiency of predator control and reduce the potential harm to native non-target animals. Increasing bait uptake must also be considered carefully in the context of the resident dingo population, estimated to number fewer than 60 individuals (E.G. Ritchie, unpubl. data). Although our study recorded only one dingo at a bait station, any bait taken by dingoes in this area is likely to have a significantly detrimental impact on this small population.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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