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Experimentally testing the response of feral cats and their prey to poison baiting

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Abstract

Context Feral cats *Felis catus* have caused the decline and extinction of many species worldwide, particularly on islands and in Australia where native species are generally naïve to the threat of this introduced predator. Effectively reducing cat populations to protect wildlife is challenging because cats have a cryptic nature, high reproductive rate and strong reinvasion ability.

Aims We experimentally tested the response of feral cats and their native prey to an *Eradicat*® poison baiting program at a conservation reserve.

Methods Baits were distributed by hand along roads and tracks every 50 m (~10 baits km^{-2}). We used camera traps to monitor the response of cats to baiting using a repeated before-after, control-impact design over six years. We also measured introduced rabbit *Oryctolagus cuniculus* activity using sand pads and small mammal and reptile captures using pitfall trapping.

Key results Dynamic occupancy modelling revealed only modest effects of baiting on cats in two out of six years, with occupancy in the baited area decreasing from 54% to 19% in 2014 (-35%) and 89% to 63% in 2017 (-26%). Baiting effectiveness was not related to antecedent rainfall or prey availability. Bait availability was reduced by non-target interference; 73% of 41 baits were removed by non-target species. We found no evidence for persistent changes in small mammal or reptile capture rates in the baited area relative to the unbaited area over the life of the project.

Conclusions Relatively low baiting density and non-target interference with baits are likely to have reduced baiting efficacy. Further testing and refinement of ground baiting is needed, including trialling higher baiting densities and/or frequencies.

Implications We highlight key areas for future research that should benefit feral cat management not only in Australia, but also on the many islands worldwide where cats threaten native wildlife.

Keywords: cat baiting, dynamic occupancy model, impact evaluation, invasive predator, lethal control, pest control

Short summary: Feral cats are a leading cause of biodiversity loss worldwide and effective cat control remains a challenge for many land managers. We experimentally tested the response of cats and their prey to a ground baiting program over six years, but found low efficacy in terms of changes in cat occupancy and activity each year. Increasing baiting density and/or frequency may improve the efficacy of ground baiting.

Introduction

Invasive predators are a major driver of global biodiversity loss, having contributed to more than 50% of bird, mammal and reptile extinctions worldwide (Doherty *et al.* 2016). Their impacts have been greatest on islands, where prey species are typically naïve to the threat of introduced predators (Salo *et al.* 2007; Medina *et al.* 2011). Feral cats *Felis catus* are one of the most damaging species because humans have spread them across the world, they are highly adaptable to varying environmental conditions (Bengsen *et al.* 2016), and they prey on a range of birds, mammals, reptiles, amphibians and invertebrates (Bonnaud *et al.* 2011). We use the term 'feral cats' to refer to animals that live in the wild and have no direct dependence on humans. Reducing the impacts of cats on native wildlife is a key concern of conservation practitioners and scientists globally (Nogales *et al.* 2013; Shionosaki *et al.* 2015; Loss and Marra 2017; Doherty *et al.* 2017).

Management of feral cats has typically focussed on lethal control, including trapping, shooting, and poison baiting. Each of these methods rely on removing individual predators from a system to reduce or eliminate predation pressure on prey species. Cats have a high reproductive rate and ability to reinvade, so lethal control must be intensive and sustained in order to effectively reduce cat population densities (Leo *et al.* 2018; Lohr and Algar 2020). Demographic studies indicate that, on average, more than 57% of a cat population must be removed annually to reduce population densities (Hone *et al.* 2010). Achieving this in practice, though, has been challenging due to the cryptic nature of cats and their aversion to entering traps and consuming baits (Fisher *et al.* 2015). For instance, the huntability of cats (number of cats shot at as a percentage of those sighted) on Marion Island ranged from 25–44% over four years (Bloomer and Bester 1992). Low intensity trapping and removal of cats in Tasmania, Australia actually caused an increase in cat activity and relative abundance at removal sites, possibly due to immigration by neighbouring cats into vacated territories (Lazenby *et al.* 2014). In the Flinders Ranges, South Australia, the number of cat detections on cameras did not change after 40 cats were removed through trapping over two months (Stobo-Wilson *et al.* 2020). On Rota Island, spotlight hunting of cats caused a modest knockdown within the first 18 months, but the population stabilised over the next 11 months (Leo *et al.* 2018). These examples illustrate that effective cat control can be very time and labour intensive, meaning that resource and financial constraints can also hinder success.

In Australia, where cats have contributed to the extinction of more than 20 native mammal species and threaten many other birds, mammals and reptiles (Woinarski *et al.* 2015; Woinarski *et al.* 2019), there are two specially designed poison baits that can effectively reduce cat populations, dependent on environmental conditions (e.g. Johnston *et al.* 2014; Comer *et al.* 2018; Lohr and Algar 2020). *Eradicat*® and *Curiosity*® are small sausage style baits comprised of kangaroo meat, chicken fat, and digest and flavour enhancers (Algar *et al.* 2007; Johnston *et al.* 2013). *Eradicat*® is registered for use in parts of Western Australia and contains 4.5 mg of 1080 poison (sodium fluoroacetate) injected into the bait (Algar *et al.* 2007). *Curiosity*® is designed for use in southern and eastern Australia and contains a hard capsule of para-aminopropiophenone (PAPP) poison (Johnston *et al.* 2013; Johnston *et al.* 2014). *Eradicat*® is usually deployed aerially at a rate of 50 baits km^{-2}, which can reduce cat populations, although effectiveness varies between years (Algar *et al.* 2007; Richards and Algar 2010; Algar *et al.* 2011; Algar *et al.* 2013; Comer *et al.* 2018; Lohr and Algar 2020). The baits are also readily consumed by dingoes *Canis dingo* and introduced red foxes *Vulpes vulpes* and thus can also reduce their population densities (Richards and Algar 2010; Berry *et al.* 2014; Wysong *et al.* 2020b).

In addition to aerial baiting, baits can also be distributed along tracks and roads ('ground baiting'), although this approach has received less attention (but see Doherty and Algar 2015; Burrows *et al.* 2018; Lohr and Algar 2020; Fancourt *et al.* 2021). Ground baiting may be a more accessible option for smaller landholders that do not have adequate resources for aerial operations (e.g. some non-government organisations and private landholders). However, because ground baiting relies on roads and tracks for bait distribution, potential baiting densities are reduced, which may limit effectiveness. Placing baits along tracks may increase encounter rates by animals that preferentially move along tracks (Geyle *et al.* 2020; Wysong *et al.* 2020a), but by the same token the baits will be biased away from animals that rarely use tracks (Fancourt *et al.* 2021).

In this study, we experimentally tested the impacts of annual *Eradicat*® ground baiting on feral cat occupancy and activity over six years (2013–19, excluding 2015) at a conservation reserve in Western Australia. We monitored impacts of baiting on both feral cats and their prey, comparing the baited area with an unbaited control area (BACI experimental design). This project began under an experimental permit before *Eradicat*® was registered by the national regulator (Australian Pesticides and Veterinary Medicines Authority). The baiting involved an annual application of baits at a density of ~10 per km^2 (one bait every 50 m), which is 20% of that used in aerial operations. This is the maximum density that we could use and we were limited to applying baits once per year under the experimental permit. Results from the first two years of this project showed that baiting reduced cat activity in 2014, but not 2013 (Doherty and Algar 2015). We reanalyse that data here, along with additional data, to address the following research questions for 2013–2019:

1. Which species consume *Eradicat*® baits and how often?
2. Does annual ground baiting with *Eradicat*® reduce cat occupancy and activity?
3. Is baiting effectiveness related to rainfall or prey availability?
4. Have capture rates of small mammals and reptiles in the baited area changed over time relative to the unbaited area?

Methods

Study site and design

This study was conducted at Charles Darwin Reserve, a ~68,000 ha property managed for conservation by Bush Heritage Australia (-29.65, 116.97; Fig. 1). The climate is semi-arid Mediterranean and mean annual rainfall is approximately 300 mm (Wanarra weather station; Bureau of Meteorology 2020). Vegetation primarily consists of *Acacia* shrublands and *Eucalyptus* woodlands, with smaller areas of salt lakes, and granite outcrops and breakaways. The property is surrounded by Unallocated Crown Land to the south, pastoral leases to the west and north, and the Mt Gibson Wildlife Sanctuary to the east. The reserve does not have predator or herbivore exclusion fences. Cats are common in the study area and dingoes less so, whereas foxes are comparatively rare (Doherty 2015b).

The baited treatment area (~150 km^2) was located in the southern half of the reserve and the unbaited experimental control area (~100 km^2) was located in the northern half (Fig. 1). Toxic *Eradicat*® baits were distributed in the baited area once annually from 2013 to 2019. Baits were laid by hand along alternating sides of vehicle tracks at a rate of one bait every 50 m, with ~1,500 baits laid each year, resulting in a density of ~10 baits km^{-2}. Baits were not replaced once they were removed. Baiting was conducted once in each of September 2013, May 2014, June 2015, and May 2016–19. However, we do not present the 2015 data due to multiple issues with camera trap operation that year that compromised data collection. As detailed below, our analyses include using dynamic occupancy models and generalised linear mixed models (GLMMs) to assess cat responses to baiting (question 2), general linear models to assess drivers of baiting effectiveness (question 3), and GLMMs to model changes in small mammal and reptile capture rates (question 4).

Camera set-up and bait uptake trials

Cats were monitored before and after baiting each year using motion-sensing cameras. Twenty cameras each separated by ≥2 km were deployed in each of the baited and unbaited treatments. At this spacing, the cameras are unlikely to have been spatially independent for the purposes of occupancy modelling, thus the occupancy results should be interpreted as probability of site use, rather than true occupancy (MacKenzie *et al.* 2018). Most of the unbaited cameras (75%) were >9.50 km from the baited area, with the minimum distance being 5.50 km. We considered this distance large enough for the two treatments to be considered independent for cats, given that home range studies from similar Australian environments recorded mean home ranges of 2.48–22.10 km^2 (Jones and Coman 1982; Edwards *et al.* 2001; Molsher *et al.* 2005; Hilmer 2010; Bengsen *et al.* 2012), which corresponds to a home range diameter of 1.80–5.30 km (if assumed to be a circle). Although dingoes were recorded on our cameras, we do not present the data here because the treatments were too close together to be independent for dingoes, given their much larger home ranges (Harden 1985; Robley *et al.* 2010; Newsome *et al.* 2013; Allen *et al.* 2014).

The cameras used in 2013–15 were a mixture of Moultrie i60 and Scoutguard 560PV units, whereas the cameras used in 2016–19 were Reconyx HC600 Hyperfire. Equal numbers of the two camera models were deployed in each treatment in 2013–15 and assignment to locations was randomised, in order to reduce any bias. Cameras were fixed to steel posts ~30 cm above the ground and next to vehicle tracks. Cameras were programmed to take three photographs each time the sensor was triggered, with a minimum delay of one minute between triggers. To measure bait uptake (question 1), each of the 20 cameras in the baited area had a bait placed in front of it during the baiting period in 2015–19. Memory cards were collected from cameras after 1–3 weeks after the baiting and photos were inspected to assess whether baits were taken, which species were responsible, and how long after bait placement removal took place.

Feral cat occupancy and activity (question 2)

Each pre- and post-baiting monitoring session lasted for 4–6 weeks (Table S1), although some individual cameras stopped working prematurely due to battery failure or memory cards reaching capacity. Post-baiting monitoring began 1–4 weeks after baiting, except in 2016 when it began two months after baiting. In 2013–15, half of the cameras had a scent lure and the other half an audio lure, which were swapped between cameras halfway through each monitoring session. Scent lures were a fresh chicken wing encased in a PVC tube pegged to the ground, with a fresh chicken wing provided when lures were swapped. The audio lure was a small electronic device that emitted the sound of a bird tweeting (Lucky Duck, WI, USA). Only scent lures (chicken wings) were used at all cameras in 2016–19.

Photos were manually inspected, and the presence of animal species was recorded, along with the site number, date and time. We created dataframes relating to sampling effort and detection histories using the camtrapR package in R (Niedballa *et al.* 2016; R Core Team 2019). The sampling effort dataframes recorded when cameras stopped functioning prior to the end of survey periods. Two cameras were also stolen in 2013. Detection histories represented the presence or absence of a species at each camera during each successive three-day period throughout a survey. For instance, a 31-day survey would have 10 three-day sampling occasions, with the extra day excluded. We chose a three-day, rather than daily, sampling period to improve model convergence.

We used dynamic occupancy models in the unmarked package in R (Fiske and Chandler 2011) to assess changes in cat occupancy in response to baiting each year. Dynamic occupancy models use data from multiple primary periods (pre-baiting and post-baiting here) that are comprised of multiple secondary periods (three-day blocks in this case) and do not assume that the system is closed between the primary periods. This approach enables the estimation of detectability, initial site occupancy (first primary period), and colonisation and extinction probabilities, which represent changes in site occupancy between primary periods, i.e. from before to after baiting.

We analysed each year separately and used a multi-step approach by first conducting all subsets model selection on the detection component and then fitting a specific set of hypothesis-based models for the occupancy and extinction components. First, we determined whether detection probabilities were influenced by vegetation composition at each site using model selection. We calculated the proportion of five vegetation types within a 500 m radius of each camera: young shrublands (<20 years since fire), old shrublands (≥20 years since fire), woodlands, salt lakes and granite outcrops. We excluded young shrublands from the modelling because it was negatively correlated with old shrublands (Pearson's r = -0.58) and woodlands (-0.43). We fitted a global detection model containing main effects for each of the four vegetation variables, while holding occupancy, colonisation and extinction probabilities constant. For 2013 and 2014, we also included camera model (Moultrie or Scoutguard) as a potential predictor of detectability. We used the dredge function in the MuMIn package (Bartoń 2019) to fit all possible model combinations and ranked the models using Akaike's Information Criterion corrected for small sample size (AICc). For the subsequent modelling of occupancy and extinction probabilities, we used the detection variables from the model with the highest weight, which in some cases was the null model (Table S2).

To determine whether baiting had an effect on cat occupancy, we fitted and ranked a series of models that included treatment (baited/unbaited) as a predictor of initial site occupancy, extinction probability, or both. These models also included the detection covariates as per Table S2. We compared these three models to a null model that only included the detection covariates (if applicable). Because the experiment used a before-after, control-impact (BACI) design, an effect of baiting would be supported if there was an effect of treatment on extinction probability. Specifically, we would expect extinction probability from pre- to post-baiting to be higher in the baited compared to unbaited area. We discuss the results from any models with a ΔAICc ≤ 2. We used parametric bootstrapping with 1,000 simulations to derive pre- and post-baiting occupancy estimates for each treatment, which we present as means with 95% confidence intervals.

We also used generalised linear mixed models with a Gaussian distribution to assess changes in cat activity in response to baiting. The activity index was calculated by dividing the number of independent detections of cats on each camera by the number of nights the camera was active and multiplying this by 100 (i.e. number of detections per 100 trap-nights). Independent detections were photographs on the same camera that were at least 60 minutes apart. The models included fixed effects of Time (pre-/post-baiting), Treatment (baited/unbaited), and Time×Treatment. A significant interaction would support an impact of baiting on cat activity. Models also included a random effect of Site to account for repeat sampling. We fitted a separate model for each year and present parameter estimates and 95% confidence intervals. To provide further context to the occupancy and activity results, we also present in the Supplementary Materials plots of naïve occupancy, which represents the proportion of sites within each treatment where each species was detected, disregarding varying sampling effort.

Drivers and outcomes of baiting effectiveness (questions 3 and 4)

We used data on rainfall, small mammal capture rates, and introduced rabbit *Oryctolagus cuniculus* activity to assess if baiting effectiveness is related to the availability of potential prey (question 3). We calculated total rainfall for the six months (Rain_6m) and 12 months (Rain_12m) prior to each baiting event using data from a rain gauge at the reserve. We used pitfall trapping data to estimate capture rates of small mammals (Mammal_CR' number of individuals captured per trap-night) in the spring (September–November) prior to each baiting event (n = 8–16 sites). The small mammal species captured were *Notomys mitchellii, Pseudomys* *hermannsburgensis, Mus musculus* and *Sminthopsis* spp. (see Doherty *et al.* 2015 for further details). As per previous studies (e.g. Coates 2008; Weston *et al.* 2009), we used sand pads to monitor rabbits and calculated an index of rabbit activity for both the spring (Rab_spr) and winter (Rab_win) prior to each baiting event (i.e. in the previous year). The index was calculated as the proportion of days rabbits were detected on each sand pad (n = 69), averaged across all sand pads for each season. Sand pad data were not available for winter 2013 and spring 2012 and 2013. To further assess the relationship between prey availability and baiting effectiveness, we calculated a ratio (PP_ratio) by dividing Mammal_CR by mean pre-baiting cat activity across all cameras for each year, following Christensen et al. (2013). Pitfall trapping and sand pad monitoring sites were spread across baited and unbaited areas (Fig. S1), although we pooled all data for analysis to assess broadscale inter-annual variation in prey availability, and because there were few differences between treatments across years (see Results). Full details of the field sampling are provided in the Supplementary Materials.

To create a measure of baiting effectiveness for each year, we subtracted the mean difference in activity or occupancy between baited and unbaited sites pre-baiting, from the mean difference after baiting, i.e. $(After_{Unbaited} - After_{Baited}) - (Before_{Unbaited} - Before_{Baited})$ (Christie *et al.* 2019). For the occupancy metric, we used the estimates from the top ranked model for each year. Using this approach, values of 0 indicate that the difference between treatments is equal for before and after baiting. Positive values indicate a greater difference in favour of unbaited sites, i.e. occupancy decreased more in baited than unbaited sites and/or unbaited sites increased more than baited sites. Negative values indicate a greater difference in favour of baited sites, i.e. occupancy in unbaited sites decreased more than in baited sites and/or baited sites increased more than unbaited sites. As such, more positive values are indicative of a greater impact of baiting.

To test the relationship between baiting effectiveness and environmental variables, we fitted general linear models with either the occupancy or activity baiting effectiveness metric as the response variable and either Rain_6m, Rain_12m, Mammal_CR, PP_ratio, Rab_spr, or Rab_win as the predictor variable. We included only one predictor variable per model due to the small sample size (n = 4–6 years). We present model parameter estimates, 95% confidence intervals and plots of the data.

We also used generalised linear mixed models assuming a Gaussian distribution to assess if capture rates of small mammals and reptiles have changed over time in baited and unbaited areas (question 4). Data were derived from the pitfall trapping as described above and in the

Supplementary Materials. The response variable was small mammal or reptile capture rate for each spring 2012–18 (excluding 2014, when sampling was not undertaken). 2012 represents a baseline from before baiting began. We included fixed effects of Year, Treatment, and Year×Treatment, and a random effect of Site to account for repeat sampling.

Results

Bait uptake

Of the 100 baits laid in front of cameras in 2015–19, 30 could not be seen on camera due to poor placement or camera malfunction, and a further 29 baits disappeared without the event being recorded on camera. Of the remaining 41 baits, we recorded an animal interaction for 34 baits. Records of cats included one bait consumed nine hours after being laid, another bait inspected but not removed seven days after being laid, and another bait that a cat walked past without seeming to inspect it, three days after it was laid. Twenty baits were either eaten or taken away by emus *Dromaius novaehollandiae* (49% of visible baits), seven by ravens *Corvus coronoides* (17%), and one each by a fox, hopping mouse *Notomys mitchellii*, and grey currawong *Strepera versicolor*. Emus removed baits within 0–9 days of baits being laid (mean = 4.05). In one case, the bait was removed five hours after being laid. Ravens removed baits within 1–22 days (mean = 6.43) and the fox, hopping mouse and currawong removed baits three days, two days and five minutes after being laid, respectively. Twenty-six minutes after the fox consumed a bait, a fox also inspected but did not remove a bait at a neighbouring camera. One dingo was also recorded walking past a bait without seeming to inspect it. Ten baits remained in place at the end of the trial period.

Occupancy and activity

Over the six-year study, feral cats were detected at 3–18 treatment cameras and 12–19 control cameras each year (mean = 11.67 and 14.83 of 20 cameras, respectively). There was uncertainty in the impacts of baiting on cat occupancy in most years, with multiple models having ΔAICc values ≤ 2 (Table S4, Fig. S2). There was only one year with a clear impact of baiting on cat occupancy: in 2017 occupancy decreased in the baited area post-baiting (from 0.89 to 0.63 in the top model), whereas it increased slightly in the unbaited area (0.89 to 1.00; Fig. 2). The changes in activity and naïve occupancy also support an impact of baiting in 2017, including a significant Time×Treatment interaction in the mixed model (Fig. 2 & S3, Table S5).

The best supported occupancy models for 2014 and 2019 also indicated greater declines in occupancy in the baited compared to unbaited area (Fig. 2), although the null models were also well supported (Table S4, Fig. S2). Changes in naïve occupancy and the activity index support an impact of baiting in 2014, but not 2019 (Fig. 2 & S3). The Time×Treatment interaction for activity in 2014 had confidence intervals slightly overlapping zero (-0.48–5.56; Table S5). Estimated occupancy from the top model for 2014 was 0.54 in both treatments pre-baiting and 0.48 in the unbaited area and 0.19 in the baited area post-baiting (Fig. 2). The activity confidence intervals for Time×Treatment in 2013 and 2018 also only slightly overlapped zero (Table S5), but when considered together with the occupancy data, there is little support for an impact of baiting.

Drivers and outcomes of baiting effectiveness

Pre-baiting occupancy, activity and naïve occupancy were similar between baited and unbaited treatments each year from 2014 to 2019 (Fig. 2 & S3), indicating that there was no cumulative effect of baiting on cat activity or occupancy over time. There was no relationship between baiting effectiveness (based on changes in cat activity/occupancy) and rainfall, small mammal capture rate, rabbit activity, or the predator-prey ration index (Table S6, Fig. S4). Small mammal capture rates were similar between treatments every year, except in 2015 and 2016 when average capture rates were 2.1- and 1.8-fold higher, respectively, at baited compared to unbaited sites (Fig. 3, Table S7). Mean capture rates of reptiles did not vary between treatments, but overall capture rates in 2013 and 2016–18 were lower than the baseline year of 2012 (Fig. 3, Table S7).

Discussion

We experimentally tested the impact of poison baiting on feral cats and potential benefits for their native prey at a conservation reserve over six years. Annual ground baiting using *Eradicat*® at ~ 10 baits km^{-2} was mostly ineffective at reducing cat occupancy, with there being only weak treatment effects in two out of the six years tested (absolute decreases in occupancy of 35% in 2014 and 26% in 2017). Consistent with the limited effect of baiting on feral cats, we found no evidence of benefits for their native prey. There are a number of factors that could have limited the efficacy of the baiting program, including baiting density, prey availability and non-target uptake of baits.

The baiting density achieved in this project was ~10 baits km^{-2}, which is much lower than the rate of 50 baits km^{-2} used in aerial operations. The lower baiting density may be insufficient for the majority of cats to detect baits or to encounter a bait when they are likely to eat it. At Matuwa in central Western Australia, ground baiting at ~2.80 baits km^{-2} was less effective than aerial baiting at 50 baits km^{-2} (Lohr and Algar 2020). In the Gibson Desert, Burrows et al. (2003) found that a fresh meat bait designed for cats reduced activity by 75% and 100% at densities of

10 and 22 baits km^{-2}, respectively, during low rainfall periods, whereas baiting at 11 baits km^{-2} during a high rainfall period reduced activity by 25%. Ground application of fresh meat baits at a density of 7.3 km^{-2} was ineffective at reducing cat densities in Queensland (Fancourt *et al.* 2021). In South Australia, Moseby & Hill (2011) tested aerial *Eradicat*® baiting at densities of 10 and 25 baits km^{-2} and found that cat activity declined in response to baiting in just one of seven trials. When taken together, these studies suggest that a baiting density of 10 baits km^{-2} is not in itself insufficient, but may be when combined with other factors, as discussed below.

The effective baiting density in our study was likely reduced by non-target consumption of baits. Our uptake trials in 2013–14 (reported in Doherty and Algar 2015) showed that corvids *Corvus* spp. removed the most baits (12 of 30), followed by cats (6) and varanids *Varanus* spp. (2). In 2015–19, 73% of the baits where fate could be determined were removed by non-target species, primarily emus, which removed 49% of visible baits. We only recorded one bait being removed by a cat. Our effective sample size was modest (41 baits) because fate could not be determined for a large number of baits, but if we assume that none of those baits were taken by non-targets (which is unlikely), then an absolute minimum of 30% of baits were removed by non-target species. Of the baits removed by non-targets, 47% were removed within three days of being laid and 90% within seven days. This means that the window of bait availability to cats is very narrow and when combined with the already low propensity of cats to consume baits, the chances of bait uptake are very low.

Many other studies have also recorded high non-target uptake of cat baits, including 22% of baits at Peron Peninsula (Algar *et al.* 2007), 14–57% at Arid Recovery (Moseby *et al.* 2011), 71% at Kangaroo Island (Hohnen *et al.* 2020), and 97% at Dryandra and Tutanning (Friend *et al.* 2020). Only one of those studies recorded emus removing baits (Algar *et al.* 2007), although it is not clear what proportion of baits were interfered with. Emus commonly travel long distances along tracks at our study site and elsewhere (TSD, *personal observation*), which would provide them with ample opportunity to encounter baits, which were placed at 50-m intervals. However, it is also worth noting that baits for the uptake trials were placed in the open to facilitate camera monitoring, which may have increased their detection and hence removal by non-target species. Moseby et al. (2011) found that bait removal by corvids was higher for baits in the open compared to those under bushes. In practice, most of the 1,500 baits deployed each year were placed underneath or close to shrubs, thus actual rates of non-target removal may have been lower. We recommend that future work quantify rates of non-target removal for baits that are placed in the open and under shrubs, and on and off tracks.

Prey availability is one of the strongest determinants of the efficacy of cat baiting programs, which itself is primarily driven by rainfall in arid and semi-arid Australia (Letnic and Dickman 2010). Using data from three sites in Western Australia, Christensen et al. (2013) showed that the efficacy of aerial cat baiting was predicted by a predator-prey ratio index. Reductions in cat activity were greatest when the amount of prey available per cat was lowest (as inferred from indices; Christensen *et al.* 2013). Short et al. (1997) also found that bait uptake by cats was inversely related to rabbit density. In contrast, we found no relationship between baiting effectiveness and a similar predator-prey index, nor with measures of rainfall, rabbit activity, or small mammal capture rate. However, this does not mean that prey availability is not important in our study area. It may just be that small sample sizes and low bait availability (and hence effectiveness) inhibited the detection of any trends. A larger sample size covering a greater range of baiting effectiveness would provide more detailed insights.

Other factors that could have limited the efficacy on ground baiting in this study include the relatively small area that was baited and the fact that baits were only applied once per year. The size of our baited area (~15,000 ha) was dictated by the need to fit both the treatment and control areas within the one property. Over time, any effects of baiting would have been reversed as cats from surrounding unbaited areas reinvaded the baited area (Algar *et al.* 2013; Lazenby *et al.* 2014). However, this does not preclude the detection of short-term effects of baiting (within 1–2 months) and we did indeed detect modest effects of baiting in two out of six years. Increasing the frequency at which baits are laid may improve the chances that cats encounter and consume baits. However, only a single annual application of baits was permitted under our experimental permit, and autumn baiting is recommended in the semi-arid zone due to lower prey availability at that time of year. Applying baits more frequently during this time could increase the amount of time that fresh baits are available and thus the likelihood that cats encounter baits when they are hungry or are using tracks (Algar *et al.* 2007).

A strength of this study was the inclusion of an unbaited reference area for comparison, allowing treatment effects to be separated from seasonal effects that could otherwise bias conclusions. For instance, if we did not survey an unbaited control area, we could have concluded that baiting was effective in 2018 and 2019, even though decreases in activity and occupancy were similar between baited and unbaited areas. We recommend that future work, where feasible, include an unbaited reference area to maximise inferential strength (Christie *et al.* 2019). This is especially important where control techniques are still being developed, or widespread and consistent effectiveness has not yet been demonstrated. However, where inclusion of an unbaited reference area is not feasible, GPS/VHF tracking of target animals to record survival post-baiting can provide complementary information about baiting efficacy.

Controlling predators is only a means to an end and the ultimate aim of any invasive predator control program should be to produce positive outcomes for the target asset, such as increased species richness, abundance, or threatened species survival. Small mammals and reptiles, along with rabbits, are the major components of cat diets in our study area (Doherty 2015a). We found no consistent differences in capture rates of small mammals and reptiles between baited and unbaited areas over the life of this project. Small mammal captures were higher in baited compared to unbaited areas in 2015 and 2016, but since we were unable to measure the impact of baiting on cats in 2015, it is difficult to contextualise these results. However, the overall lack of differences is not surprising given that there were only modest effects of baiting on cats in two out of six years (2014 and 2017). For cat control to benefit prey populations, reductions in cat populations must be intense and sustained, although there is little precise information about the minimum level of suppression required (Norbury *et al.* 2015). The clearest examples are where cats (and foxes) have been eradicated from islands and fenced exclosures, resulting in dramatic improvements in the survival of reintroduced mammals (Legge *et al.* 2018) and increases in the abundance and richness of resident fauna (Moseby *et al.* 2009; Roshier *et al.* 2020). Although there are many studies demonstrating reductions in cat activity or density in response to baiting, there is very little evidence available regarding the outcomes for prey populations (but see Stewart *et al.* 2019; Comer *et al.* 2020). We recommend that control programs for cats—and other pest species more generally—incorporate clear objectives and monitoring programs for the species they are trying to protect (see also Reddiex and Forsyth 2006). Such monitoring can enable assessment of return-on-investment and adaptive management to refine interventions over time, including detecting and addressing unexpected negative consequences (Ruscoe *et al.* 2011; Walsh *et al.* 2012).

Feral cat management is challenging, and the effectiveness of different approaches varies between locations and years. Further work is clearly needed to improve the effectiveness of ground baiting of feral cats. Key areas for future research are investigation of methods to reduce non-target removal of baits; investigation of methods that improve bait detection and consumption by cats; and assessment of different baiting densities and frequencies. Furthermore, since effective baiting may selectively target only a subset of the population (e.g. poor hunters or bait naïve cats; Lohr and Algar 2020), complementing baiting with other control methods such as trapping and shooting may be important to maximise the impacts of control efforts and to reduce the risk of selecting for bait resistance (Allsop *et al.* 2017; Lohr and

Algar 2020). In addition, research on the effects of managing the environment by either reducing the resources supporting cat populations (e.g. rabbit populations; McGregor *et al.* 2020), or managing fire and grazing to conserve habitat structure that provides refuges for native species (Leahy *et al.* 2016; Legge *et al.* 2019), could help identify the most effective approaches for feral cat management. Such work would benefit feral cat management not only in Australia, but also on the many islands worldwide where cats threaten native wildlife.

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Data availability Data and code are available at FigShare https://doi.org/10.6084/m9.figshare.13240637.v1

Authors' contributions TSD conceived and designed the research; all authors collected the data; TSD analysed the data and wrote the manuscript, with input from all co-authors.

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Figure captions

Figure 1. Map of the study site and camera trap locations, with the smaller map showing location within Western Australia.

Figure 2. Feral cat occupancy (top row) and activity (bottom row) for the baited and unbaited areas each year. Symbols represent means and error bars represent 95% confidence intervals.

The dotted boxes around 2014 and 2017 represent years where the data support an impact of baiting.

Figure 3. Capture rates (number of individuals captured per trap per night) of small mammals and reptiles at baited and unbaited pitfall trapping sites. Symbols represent treatment means and vertical lines are 95% confidence intervals.

Supplementary materials

Table S1. Dates of monitoring periods and baiting in each year of the project.

Year	Pre-baiting	Baiting	Post-baiting
2013	9 Aug – 7 Sep	8 Sep	1 Oct – 6 Nov
2014	2 Apr – 9 May	11 May	20 May – 18 Jun
2015*	8 Apr – 8 May	5 June	19 Jun – 1 Aug
2016	30 Mar – 4 May	12 May	9 Jul – 7 Aug
2017	10 Apr – 12 May	19 May	26 May – 26 Jun
2018	3 Apr – 2 May	8 May	15 May – 13 Jun
2019	3 Apr – 2 May	8 May	15 May – 13 Jun

*As described in the methods, we do not present or analyse the 2015 data, but include the dates here for comprehensiveness.

Table S2. Detection covariates used in cat occupancy modelling.

Year	Covariates
2013	Shrub_old
2014	Shrub_old + Woodland
2016	Shrub_old + Salt_lake
2017	None
2018	Shrub_old + Salt_lake
2019	None

Additional details about pitfall trapping and sand pad monitoring

We used pitfall trapping data to estimate capture rates of small mammals and reptiles in the spring (September–November) prior to each baiting event. Small mammals were sampled at 6–16 pitfall trapping sites each year. Sites were split between young (8 to 20 years since last fire) and old (26 to >55 year since last fire) shrublands (Table S3, Fig. S1). Each site consisted of two parallel 25-cm high aluminum drift fences 60 m in length and separated by ~30 m. Six pitfall traps (4 x 20-L buckets and 2 x 15-cm diameter PVC pipes) were situated at 10-m intervals along the fences. Sites were sampled for 10 nights each in 2012 and 2013, and 4–5 nights in 2015–18 (mean = 4.3), so we truncated the earlier data to the first five nights of trapping. We calculated small mammal capture rates for each year as the number of individuals captured at each site divided by the number of trap-nights (number of nights × number of traps).

Table S3. Number of pitfall trapping sites in young (8 to 20 years since last fire) and old (26 to >55 year since last fire) shrublands sampled each year.

Year	Young shrublands	Old shrublands	Total sites
2012	8	8	16
2013	8	8	16
2015	4	4	8
2016	8	7	15
2017	7	6	13
2018	8	7	15

We used sand pad monitoring data to calculate an index of rabbit activity for both the spring and winter seasons prior to each baiting event (i.e. in the previous year). There was a circuit of 69 sand pads separated by 1–2 km each (Fig. S1), which were monitored for 3–6 days in each season and the presence/absence of rabbits and other animals was recorded each morning. The index was calculated as the proportion of days rabbits were detected on each sand pad, averaged across all sand pads. Sand pad data were not available for winter 2013 and spring 2012 and 2013.

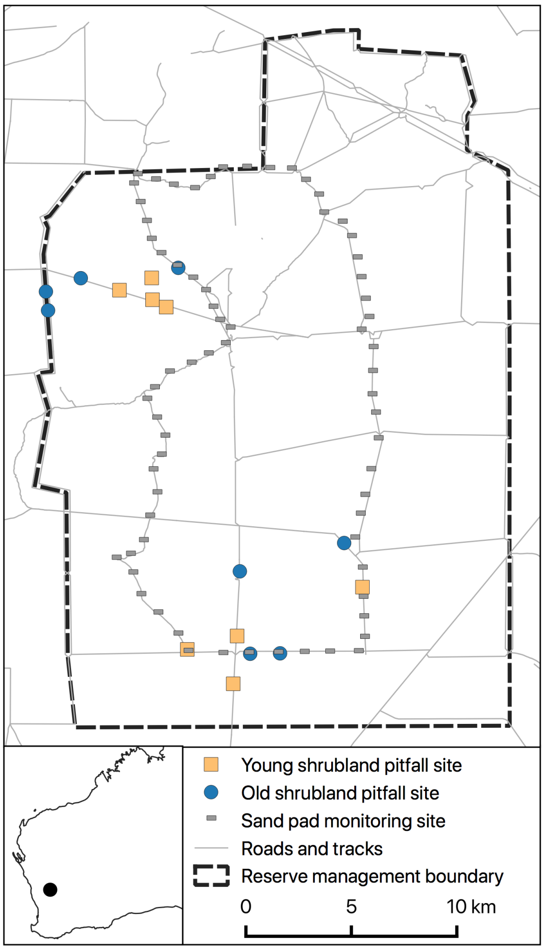

Figure S1. Map of the study site, pitfall trapping sites and sand pads, with the smaller map showing location within Western Australia.

Table S4. Dynamic occupancy modelling results for feral cats. Only models with a ΔAICc ≤ 2 are shown. ψ, initial occupancy; ε, extinction probability.

Year	Model	ΔAICc	Weight
2013	$\psi \sim$ Treatment, $\varepsilon \sim 1$	0	0.44
	$\psi \sim 1$, $\varepsilon \sim$ Treatment	1.52	0.21
	$\psi \sim 1$, $\varepsilon \sim 1$	1.69	0.19
	$\psi \sim$ Treatment, $\varepsilon \sim$ Treatment	2.00	0.16
2014	$\psi \sim 1$, $\varepsilon \sim$ Treatment	0	0.29
	$\psi \sim 1$, $\varepsilon \sim 1$	0.10	0.28
	$\psi \sim$ Treatment, $\varepsilon \sim 1$	0.57	0.22
	$\psi \sim$ Treatment, $\varepsilon \sim$ Treatment	0.72	0.20
2016	$\psi \sim 1$, $\varepsilon \sim 1$	0	0.48
	$\psi \sim$ Treatment, $\varepsilon \sim 1$	1.55	0.22
	$\psi \sim 1$, $\varepsilon \sim$ Treatment	1.71	0.20
2017	$\psi \sim 1$, $\varepsilon \sim$ Treatment	0	1.56
	$\psi \sim$ Treatment, $\varepsilon \sim$ Treatment	1.40	0.28
2018	$\psi \sim 1$, $\varepsilon \sim 1$	0	0.45
	$\psi \sim 1$, $\varepsilon \sim$ Treatment	1.16	0.25
	$\psi \sim$ Treatment, $\varepsilon \sim 1$	1.86	0.18
2019	$\psi \sim 1$, $\varepsilon \sim$ Treatment	0	0.47
	$\psi \sim 1$, $\varepsilon \sim 1$	1.40	0.23
	$\psi \sim$ Treatment, $\varepsilon \sim$ Treatment	2.00	0.17

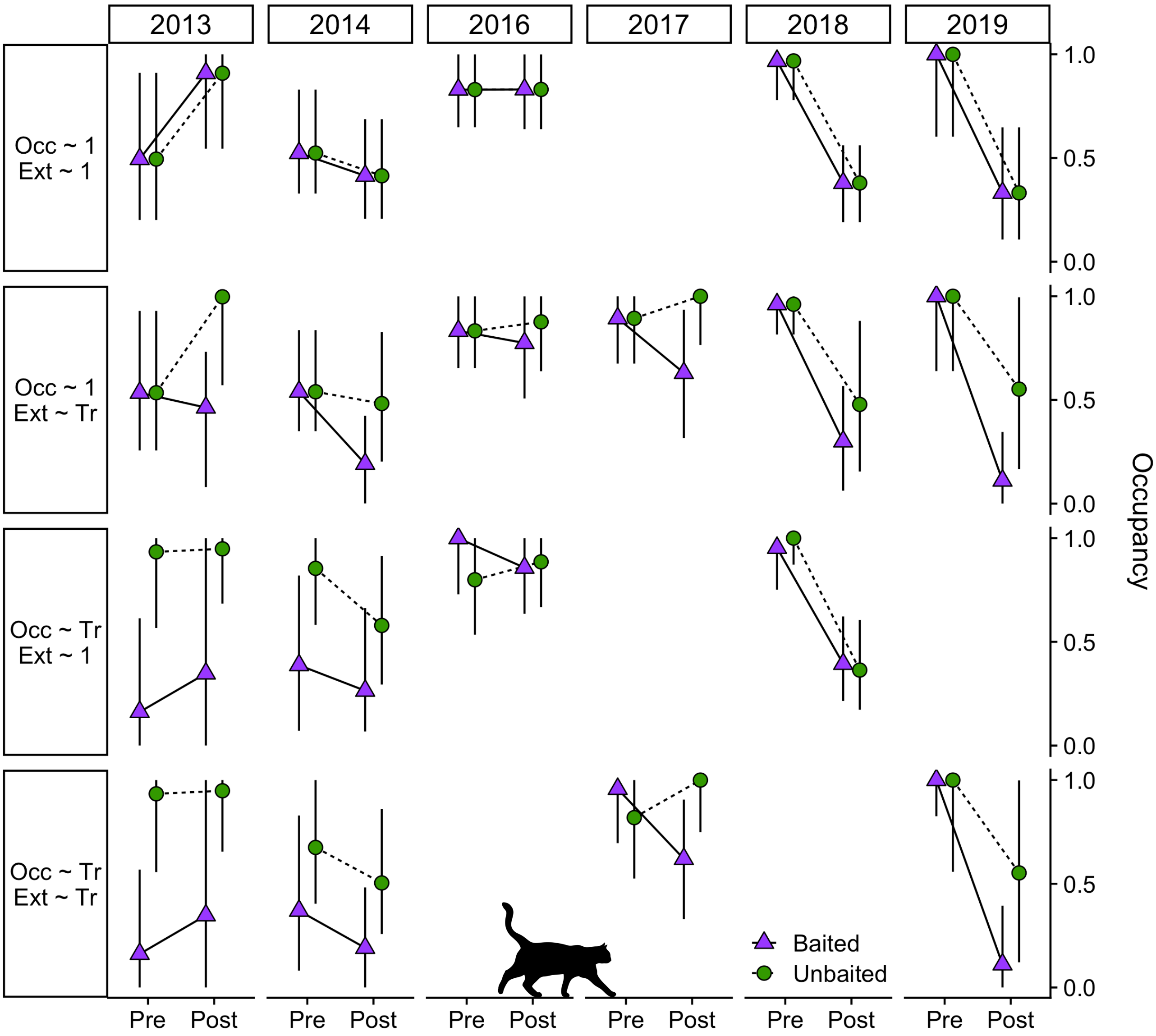

Figure S2. Estimated cat occupancy for all well supported models (ΔAICc ≤ 2) in each year. Occ, initial occupancy; Ext, extinction probability; Tr, treatment (baited/unbaited). Symbols represent means and bars represent 95% confidence intervals.

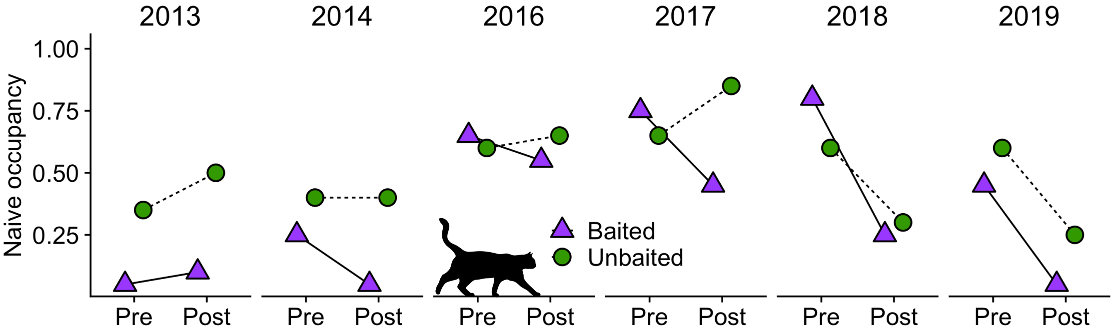

Figure S3. Naïve occupancy of cats (proportion of sites with cats present) pre- and post-baiting each year.

Table S5. Mixed modelling results for changes in cat activity in response to poison baiting. Values in cells are model parameter estimates and 95% confidence intervals are provided in parentheses. Time represents before or after baiting, Treatment represents baited or unbaited, and Interaction represents the interaction those two fixed effects. Bold text indicates variables where the 95% confidence intervals do not overlap zero.

Year	Intercept	Time	Treatment	Time×Treatment
2013	0.19 (-1.36 – 1.74)	0.10 (-2.06 – 2.26)	1.21 (-0.92 – 3.35)	2.76 (-0.24 – 5.76)
2014	1.17 (-0.86 – 3.21)	-1.00 (-3.14 – 1.13)	1.28 (-1.57 – 4.13)	2.54 (-0.48 – 5.56)
2016	5.04 (2.97 – 7.11)	-2.10 (-4.34 – 0.14)	-0.80 (-3.70 – 2.09)	2.77 (-0.61 – 6.16)
2017	4.79 (3.06 – 6.52)	**-2.84 (-5.18 – -0.50)**	-0.55 (-2.96 – 1.87)	**3.44 (0.18 – 6.70)**
2018	5.50 (4.08 – 6.92)	**-4.17 (-6.18 – -2.16)**	-1.99 (-4.03 – 0.05)	1.99 (-0.87 – 4.85)
2019	1.53 (0.49 – 2.57)	**-1.37 (-2.70 – -0.03)**	**1.64 (0.17 – 3.11)**	-0.56 (-2.45 – 1.32)

Table S6. General linear modelling results for the effect of environmental variables on baiting effectiveness. Values in cells are model parameter estimates and 95% confidence intervals are provided in parentheses. Rain_6m, total rainfall for the six months prior to baiting; Rain_12, total rainfall for the 12 months prior to baiting; Mammal_CR, capture rate of small mammals for spring prior to baiting; PP_ratio, ratio of prey availability to predator activity (see Methods); Rab_win, rabbit activity index for winter prior to baiting; Rab_spr, rabbit activity index for spring prior to baiting.

Predictor	Occupancy	Activity
Rain_6m (n = 6)	-0.0002 (-0.004 – 0.004)	0.01 (-0.01 – 0.03)
Rain_12m (n = 6)	0.001 (-0.003 – 0.004)	0.01 (-0.01 – 0.02)
Mammal_CR (n = 6)	-3.04 (-19.07 – 12.99)	11.77 (-75.10 – 98.64)
PP_ratio (n = 6)	-9.08 (-20.98 – 2.81)	10.93 (-68.19 – 90.05)
Rab_win (n = 5)	-1.80 (-6.84 – 3.23)	3.06 (-26.77 – 32.89)
Rab_spr (n = 4)	2.54 (-0.74 – 5.81)	5.68 (-27.44 – 38.81)

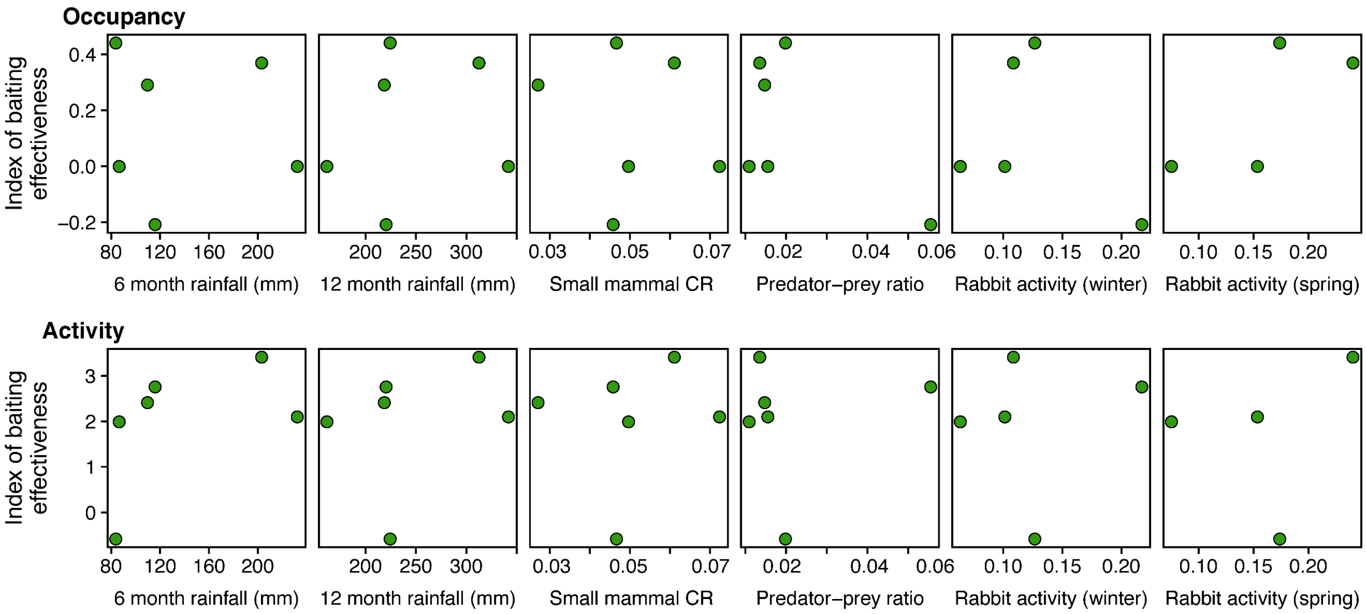

Figure S4. Relationships between baiting effectiveness and environmental variables. The top row relates to occupancy and the bottom row relates to activity. Values of 0 for the baiting effectiveness index indicate that the difference between treatments is equal for before and after baiting. Positive values indicate a greater difference in favour of control sites, i.e. impact sites decreased more than control sites and/or control sites increased more than impact sites. Negative values indicate a greater difference in favour of impact sites, i.e. control sites decreased more than impact sites and/or impact sites increased more than control sites.

Table S7. Generalised linear mixed modelling results relating to differences in capture rates (CR) of small mammals and reptiles in response to Year, Treatment and the interaction. Values in cells are model parameter estimates and 95% confidence intervals are provided in parentheses. Bold text indicates predictor variables where the 95% confidence intervals do not overlap zero. The reference levels used for the intercept were 2012 and Baited.

Predictor	Level	Mammal_CR	Reptile_CR
Intercept	2012, Baited	0.03 (0.00 – 0.06)	0.24 (0.19 – 0.29)
Year	2013	-0.01 (-0.05 – 0.04)	**-0.10 (-0.17 – -0.04)**
	2015	**0.08 (0.02 – 0.13)**	-0.07 (-0.16 – 0.02)
	2016	**0.05 (0.008 – 0.09)**	**-0.19 (-0.19 – -0.05)**
	2017	0.02 (-0.02 – 0.06)	**-0.20 (-0.27 – -0.13)**
	2018	0.02 (-0.02 – 0.06)	**-0.17 (-0.24 – -0.10)**
Treatment	Unbaited	0.03 (-0.01 – 0.07)	-0.05 (-0.12 – 0.02)
Interaction	2013×Unbaited	-0.02 (-0.08 – 0.04)	0.05 (-0.05 – 0.14)
	2015×Unbaited	**-0.09 (-0.16 – -0.02)**	0.10 (-0.02 – 0.22)
	2016×Unbaited	**-0.06 (-0.12 – -0.01)**	0.01 (-0.08 – 0.10)
	2017×Unbaited	-0.03 (-0.09 – 0.03)	0.04 (-0.06 – 0.13)
	2018×Unbaited	-0.04 (-0.10 – 0.02)	0.08 (-0.01 – 0.17)