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Bangers and Cash: Baiting Efficiency in a Heterogeneous Population

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ABSTRACT Uptake of baits is a key variable in management actions aimed at the vaccination, training, or control of many vertebrate species. Increasingly, however, it is apparent that individuals of the target species vary in their likelihood of taking baits. To optimize a baiting program, knowledge on the rate of bait uptake, how this rate changes with bait availability, and the proportion of the target population that will take a bait is required. The invasive cane toad (*Rhinella marina*) in Australia is a major threat to northern quolls (*Dasyurus hallucatus*), which are poisoned when they attack this novel toxic prey item. Conditioned-taste-aversion baits (cane toad sausages) can be delivered in the field to train northern quolls to avoid toads. We conducted a large-scale field trial among 11 sites across one large property in Western Australia from 19–26 July 2017. We used camera traps and statistical modelling to estimate the proportion of baitable animals in the population, their encounter rate with baits, and survival rate of baits in the environment. Population estimates varied at each site from 2.5 to 16.8 quolls per site, resulting in a range among sites of 0.7–4.6 baits available/individual. Approximately 64% of individual quolls were bait-susceptible. Both encounter rate and bait survival were low, resulting in our baiting regime treating <30% of the bait-susceptible population. Using our model parameters, we estimate that we would need to increase our bait density 6-fold to treat all bait-susceptible individuals in the population. Without accounting for heterogeneity in bait-susceptibility, our model would suggest we would need a 10-fold increase in bait density. Thus, accounting for heterogeneity provides a more efficient baiting design. Data and models such as ours provide wildlife managers with information critical to informed decision-making and are fundamental to estimate the cost-efficiency of any baiting campaign.

KEYWORDS bait uptake, *Bufo marinus*, conditioned taste aversion, *Dasyurus hallucatus*, invasive species, *Rhinella marina*.

Globally, many populations of wildlife are intensively managed, and the delivery of baits is an important management tool in this context (Bomford and O'Brien 1995). Uptake of doses of toxic or nontoxic compounds in baits is a necessity in the vaccination (Henning et al. 2017), training (Gentle et al. 2004, Cagnacci et al. 2005), control (Kirkpatrick and Turner 1985) and eradication (Moseby et al. 2011, Dundas et al. 2014, Johnston et al. 2014, Kimball et al. 2016) of many vertebrate species.

A successful baiting program is one that is cost-effective and results in a large proportion of target individuals taking bait (Thomson 1986). Significant progress has been made with the technical aspects of delivering a baiting program, such that baiting can typically be achieved inexpensively and without complex tools or training (Avery et al. 1995). Aircraft, for example, can provide an efficient and fast means of distributing baits over large or otherwise inaccessible tracts of country (Thomson 1986). Success is mostly hampered by the attractiveness and palatability of baits or willingness of individuals in the population to consume baits. It is increasingly appreciated, for example, that some individuals may be less bait-susceptible because they are neophobic, bait-shy, or otherwise uninterested when their usual diet is abundant (Birch 1999, Francis et al. 2003, Mappes et al. 2005, Kelly and Phillips 2017).

Estimating the heterogeneity across a population in the propensity to take baits is a useful first step in assessing a baiting program. A useful second step is to optimize bait delivery by determining the fewest baits required to achieve a given proportion of the population baited. These aims require data on bait uptake within the target population and how this changes with density of baits delivered into the

landscape. Collection of these data is often logistically difficult and costly.

Consequently, management decisions are often made based on operator experience rather than empirical evidence (Cook et al. 2010). Remote monitoring tools (such as camera traps) offer a cost-effective means to acquire relevant data, but these data do come with analysis challenges. We estimated key parameters (such as the proportion of baitable individuals, the survival rate of baits once deployed into the environment, and the effect of bait density on uptake probability) from mark–recapture data acquired from camera traps.

Cane toads (*Rhinella marina*) were introduced in northeastern Australia in 1935 and have since rapidly expanded across the north of Australia (Phillips et al. 2007). These toads carry with them a suite of defensive toxins—Bufadienolides—unlike toxins possessed by native Australian animals. As a result, many vertebrate predators, including northern quolls (*Dasyurus hallucatus*), die after attacking or consuming toads (Webb et al. 2005, 2011; Smith and Phillips 2006; Hayes et al. 2009; Shine 2010). Northern quolls are now listed as federally endangered as a consequence of the toad invasion. The delivery of conditioned-taste-aversion baits (cane toad sausages) can, however, be used to train individual northern quolls to avoid toxic invasive cane toads (Indigo et al. 2018). Conditioned-taste-aversion (CTA) is a powerful innate response that has evolved as a defense mechanism against poisoning (Conover 1995, Cohn and MacPhail 1996, Mappes et al. 2005, Page and Ryan 2005, Glendinning 2007) and results in an animal acquiring an aversion to a referent food as a result of a nauseating or unpleasant experience (Gustavson and Nicolaus 1987). There is currently intense interest in training native Australian predators to avoid cane toads (O'Donnell et al. 2010, Webb et al. 2015, Ward-Fear et al. 2016, Jolly et al. 2017, Kelly and Phillips 2017). Previous research by Indigo et al. (2018) showed that

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quolls consuming a cane toad sausage reduced their attack behaviour toward, and overall interest in, cane toads. Importantly, bait uptake by quolls was also observed when baits were delivered under a realistic field scenario.

Conditioned-taste-aversion baiting on a landscape scale is a relatively new technology. Thus the importance of developing evidence-based predictions to guide decision-makers is imperative (Jackson et al. 2007). In many ways, though, it is simply a new baiting technology, so methods developed for assessing CTA baits apply equally to any other bait. Here, we develop an analysis using camera-trap data to estimate the proportion of baitable individuals and how uptake probability changes with bait availability.

STUDY AREA

We conducted the study in the Artesian Range section (~170,000 ha) of Charnley River–Artesian Range Wildlife Sanctuary (16°24'S, 125°30'E; 300,000 ha), a property managed by the Australian Wildlife Conservancy (AWC) in the Kimberley region of Western Australia for conservation. We worked at 11 sites on the property (Fig. 1); from 07/19/2019-07/26/2019. Sites were selected based on the detection of quolls in the Australian Wildlife Conservancy's fauna surveys (J.Smith, Australian Wildlife Conservancy, unpublished data). Each site was separated by ≥ 5 km to maximize independence between sites. The sites were characterized by savanna woodland with a perennial grass layer, dissected by sandstone gorges of varying topographic complexity. Vegetation of the study areas was dominated by eucalypt woodland, with a grass layer composed of both perennial (*Triodia* spp., *Dicanthium* spp., *Aristida* spp., *Chrysopogon fallax*, *Sehima nervosum*, *Themeda traianandra*) and annual species (*Sorghum stipodeum*). This area has a tropical monsoon climate and on

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average receives 788–900 mm of rain annually, most of which falls from December to March. At the time of the study, there was no rainfall and the mean temperature was 27.5 degrees Celsius; additionally, toads were yet to arrive at any of our sites.

METHODS

Cane Toad Sausages

We made cane toad sausages using 15 g of minced skinned adult cane toad legs, 1 whole cane toad metamorph (weighing <2 g), and 0.06 g of Thiabendazole (per sausage; dose rate <300 mg/kg adult quoll body mass, determined by the smallest—200 g—adult measured at our study site), all packed into a synthetic sausage skin and deployed fresh (Indigo et al. 2018). Thiabendazole is an inexpensive, broad-spectrum anthelmintic and antifungal agent (Robinson et al. 1965). It is orally effective and regarded as relatively safe, producing low mammalian mortality: oral LD₅₀ is 2.7g/kg body weight (Dilov et al. 1982). Thiabendazole induces a robust CTA after a single oral dose (Nachman and Ashe 1973, O'Donnell et al. 2010) and is physically stable at ambient conditions in the bait substrate (Gill et al. 2000, Massei et al. 2003).

Bait Stations

We defined “site” as the location where we deployed an array of bait stations and cameras. “Bait station” was a location within a site where bait was offered. A “session” was a time interval when bait stations were active. We conducted one session over the course of an 8-day period. Each session recorded 2 “bait events,” where new bait was placed unsecured at a bait station and the old bait removed. There were 2 baiting events—BE1 and BE2. We used a highly attractive nontoxic bait during BE1 (days 0–3) to estimate population size at each site. We used the bait of

interest (a toad sausage intended to make an animal sick) during BE2 (days 4–7). We used data from this second session to estimate bait-uptake probability conditional on the population size estimated in BE1.

Each site contained 12 bait stations placed 100–120 m apart in a 4×3 grid-plot array. A single camera trap (white flash and Infrared Motion Activated, HP800; Reconyx, Holmen, Wisconsin, USA) was placed at each bait station. To habituate quolls to the provisioning of bait in the first bait event (BE1), we used peanut butter (Kraft Heinz Company, South Melbourne, VIC, Australia) and mackerel in brine as bait (Homebrand; Woolworths, Australia Ltd, Bella Vista, NSW, Australia), available for 4 nights (Hohnen et al. 2013, Austin et al. 2017). In the second bait event (BE2), we made cane toad sausage baits available at the bait station for 4 nights.

We secured cameras to trees or rocky ledges approximately 1 m from the ground and aligned them to face directly downward (Hohnen et al. 2013, Diete et al. 2016). We set cameras to take 5 consecutive photographs for each trigger with no delay between triggers. We placed each bait inside a ring of powdered insecticide (Coopex, Leverkusen, Germany) to protect from ant spoilage. We deployed 132 individual cane toad sausages across the 11 sites over the period of study.

Camera-trap Data Collation

We collated images from bait stations and recorded the ID of the individual for each individual pass, and (in BE2) whether the bait was taken. We recorded which species (and individuals in the case of quolls) were attracted to bait, and which species (and individuals) took bait. We identified individual quolls visiting bait stations by their unique spot patterns to determine visitation rate and bait uptake (Hohnen et al. 2013). To do this we employed Wild ID software (Version 1.0, Jan 2011), which extracts

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distinctive image features in animals spot patterns (Bolger et al. 2011). The program calculates a matching score that characterizes the goodness-of-fit between 2 images. We then used these matching scores to rank and select matches to each focal image. We also conducted manual checks with all photographs and compared them with those already identified to determine whether a new individual had been recorded. We identified quolls were identified to individual within each site. We treated each site (separated by a min. of 5 km) as independent with regard to quoll ID and behaviour.

We conducted the study under Wildlife Conservation Regulation 17 (Permit number: SFO10584), and it was approved by the University of Technology Sydney Animal Care and Ethics Committee (Protocol: 2012-432A) and Department of Parks and Wildlife Animal Ethics Committee (Protocol: AEC 2016_50 and Protocol 2013_37). Additionally, this study was conducted in accordance with the approved outline submitted to the AVPMA, Permit number: PER 82262.

Statistical Analysis

We assume that there are 2 classes of individuals: those that will take a bait given the opportunity and those that will not. We denote the number of individuals at site j , N_j . We are interested in estimating the proportion of N_j that are initially bait-susceptible, z , and the proportion of baitable individuals that take a bait under our baiting strategy, u . This latter proportion can be made a function of bait longevity and baiting density (see details below).

In our first baiting event (BE1), our observations consist of a sighting history for each observed individual quoll over 4 nights of camera-trapping at the site. In our second baiting event (BE2), we record when individuals at a site took a bait. To estimate N_j we used a closed population mark–recapture analysis in which each

individual (denoted i) was either observed or not according to a draw from a Bernoulli distribution:

$$O_{it_1} \sim \text{Bernoulli}(d_{t_1})$$

where t_1 indexes day within the first baiting session ($t_1 \in \{0,1,2,\dots,3\}$). Previous experience with quolls showed that detection rate of individuals declines over time (Smith et al. 2017); thus, we assumed that detection probability (d_{t_1} , driven by attraction to baited stations) declines over time according to

$$\text{logit}(d_{t_1}) = \mu_d + \beta_{t_1}$$

where d_{t_1} denotes the expected detection probability at time t_1 , μ_d is the expected detection probability at $t_1 = 0$, and β is the change in log odds of detection over time.

We used the “data augmentation” method in combination with this detection probability to estimate N_j for each site (Royle et al. 2007, Kéry and Schaub 2011). Data augmentation offered a flexible way to model patterns of detection probability in our closed populations (Kéry and Schaub 2011). Under this approach, data are ‘padded’ by adding an arbitrary number of zero-only encounter histories of ‘potential’ unobserved individuals. The augmented data set is modelled as a zero-inflated version of the complete-data model and changes the problem from estimating a count to estimating a proportion (i.e., the proportion of the padded number of individuals that are real; Royle et al. 2007). This was executed by adding a latent binary indicator variable, R_i , to classify each row in the augmented data matrix as a ‘real’ individual or not, where $R_i \sim \text{Bernoulli}(\omega_j)$. The parameter ω_j is estimated from these data, and $N_j = \sum \{R_{i(j)}\}$. This process allowed us—using data from the first baiting event (4 days)—to estimate population size at each site.

We used our second baiting event—in which we deployed toad-sausage

baits—to estimate the proportion of the population that took baits. The observation type here was an individual taking a bait on a particular day, $T_{i(j),t_2}$. We assumed this variable:

$$T_{i,t_2} \sim \text{Bernoulli}(u_{i,t_2})$$

where u_{i,t_2} is the mean probability of a quoll taking a bait at each $t_2 \in \{0,1,2,3\}$ within the second baiting event. This probability is made conditional on the quoll being a ‘real’ individual ($R_i = 1$) and being bait susceptible ($Z_i = 1$), such that if either of these conditions are not met, $u_i = 0$. We define a quoll’s initial susceptibility to being baited as a latent indicator variable:

$$Z_i \sim \text{Bernoulli}(z)$$

where z is the probability that an individual is bait-susceptible.

Under the condition of an individual being real and susceptible, u , is the probability of 2 events: a quoll encountering a bait, E , and taking that bait, T . Thus, $u_{i,t_2} = P(E_{t_2} \cap T_{t_2} | R_i = 1 \cap Z_i = 1)$. The probability of event E is determined by the number of baits in the landscape at a given time. Here we assume an exponential decay of baits, such that the mean number of baits at t_2 :

$$B_{t_2} = B_0 s^{t_2}$$

where B_0 is the initial number of baits deployed (at $t_2 = 0$; $B_0 = 12$ in our field trial), and s is the per-day survival probability of baits. Assuming encounters are independent, the probability that an individual encounters ≥ 1 of these baits within each time is, thus,

$$P(E_{t_2}) = 1 - (1 - \tau)^{B_{t_2}}$$

where τ is the mean probability of an individual encountering any one of the B baits.

Given that we are only considering real, susceptible individuals, the probability of taking a bait at $t_2 = 0$ is one: $P(T_0) = 1$. At $t_2 > 0$, however, we need to account for the probability that our individual may have taken a bait in one of the previous time intervals and so is no longer susceptible. If we assume that all susceptible individuals encountering a bait take the bait, and avoid baits thereafter (and dropping individual indices),

$$u_0 = P(E_0)$$

$$u_1 = P(E_1)(1-u_0)$$

$$u_2 = P(E_1)[1-(u_0 + u_1)]$$

With the general expression:

$$u_{t_2} = P(E_{t_2}) \left(1 - \sum_{k=0}^{t_2-1} u_k \right)$$

Our model contains parameters for detection probability (μ_d and β), parameters for estimating population size at each site (ω_j), and parameters that describe uptake probability in terms of initial susceptibility to baiting (z), survival rate of baits (s), and probability that an individual encounters a bait given it is present in the environment (τ).

The model described above is summarized by a Directed Acyclic Graph (DAG; Fig. 2; Clark and Gelfand 2006). These DAGs represent relationships (arrows) between observed data and unknown parameters or hypotheses of the model (nodes). The lines represent relations and hierarchy between nodes. Nodes symbolize data observed (e.g., $O_{i,(j),t}$) and parameters to estimate (e.g., s , Z , B_i). The model was fitted using Bayesian Markov Chain Monte Carlo (MCMC) methods within the package JAGS using Program R (Plummer 2016, R Core Team 2017). We used minimally informative priors except for z (Table 1). For this parameter, we had prior information

on the proportion of quolls likely to take a bait from Indigo et al. (2018). We compared the modelled output with an identical model, in which we substituted a minimally informative prior for z (Fig. 3). Parameter estimates were based on 100,000 iterations with a thinning interval of 5 following a 10,000 sample burn-in. We tested 3 MCMC chains; we assessed model convergence by eye and using the Gelman–Rubin diagnostic (Gelman and Rubin 1992).

RESULTS

Cameras at bait stations detected 86 individual quolls across our 11 sites. During BE2 (in which sausages were deployed), bait stations were visited by 45 individual quolls. Of these 45 individuals, 21 encountered a cane toad sausage with the remaining 24 animals arriving at the bait station after baits had been taken by other species or other quolls. Of these 21 CTA bait-exposed individuals, 18 individuals took the bait (Table 2). Twenty-three species were identified investigating bait stations in BE2 (Figure S1). Of these nontarget species, bait was taken by Torresian crows (*Corvus orru*; $n = 6$), common rock rat (*Zygomys argurus*; $n = 4$), northern brown bandicoot (*Isodon macrourus*; $n = 4$), skinks (*Ctenotus* spp.; $n = 3$), golden-backed tree-rat (*Mesembriomys macrurus*; $n = 1$), and an unknown rodent species ($n = 1$).

Bayesian mark–recapture population estimates (N_j) and associated credibility intervals (CI = 95%) ranged from 0 to 22 (Table 2). Baiting at the nominal rate of 1 bait/100 m² resulted in 0.71–4.69 baits available/animal at $t_2 = 0$. The probability of an individual encountering an individual bait given that the bait was present in the environment was low ($\tau = 0.018$; 95% CI = 0.009–0.03). The per-day survival probability of baits was also low, indicating very few baits available after the day of deployment ($s = 0.51$; 95% CI = 0.29–0.78).

Overall, baiting at 1 bait/100 m² resulted in bait uptake by approximately 18% of quolls at a site. But the proportion of baitable quolls z was estimated to be 0.64 (95% CI = 0.52–0.77). Thus, our baiting regime delivered baits to <30% of the bait-susceptible individuals at each site. Using parameters for bait survival and uptake probability indicated that baiting at the rate of 72 baits/7-ha site (i.e., 6 times more baits than we used) should result in essentially all baitable individuals taking bait within 5 days of bait deployment (Fig. 4). By contrast, if we assume that all individuals are baitable, our model suggests we would need to deploy >120 baits (10 times more than we used).

DISCUSSION

We used these data from camera traps (with some prior information) to estimate key parameters of interest for a quoll population: the proportion of a population that is baitable, encounter rates, and bait survival rate. These parameter estimates provide valuable information for managers considering a baiting program, allowing them to assess the likely outcome of a baiting program, optimize the baiting rate, and estimate costs. In our case, the baiting program is to train wild quolls to avoid cane toads immediately prior to the arrival of cane toads in the landscape.

We estimated that the best outcome achievable in our system is for us to deliver baits to 64% of the population. The other 36% of the population appear to not be bait-susceptible. Most of our information on this parameter comes from our prior expectation of uptake rate, derived from a combination of field and captive trials by Indigo et al. (2018). We updated our prior value for z —the variable representing the probability of being baitable with these data, to obtain the posterior value of 64%. We observed only a small shift between prior and posterior for this parameter; thus, our

new observations do not provide much additional information on this parameter, suggesting that it may be generally important to estimate this parameter using prior work. Certainly, heterogeneity in baitability should not be unexpected in wild populations. It could arise by innate variation in food selection (Birch 1999), but also through variation in boldness where some individuals may exhibit a neophobic response to bait as a consequence of genetic predisposition (Marples et al. 2007, Hoppitt and Laland 2013, Greggor et al. 2014). These predispositions might have developed as a result of early learning, experience, interactions with the environment, and feeding selection by adults (Birch 1999, Francis et al. 2003, Mappes et al. 2005, Hoppitt and Laland 2013).

Irrespective of the mechanism, nonbaitable individuals reduce the proportion of the population that are trainable with CTA. Although 64% may seem a relatively poor level of maximum bait success, we can reasonably expect that some fraction of the nonbaitable animals may also innately avoid toads. Certainly there is evidence in other taxa that some level of innate avoidance of toads is present in toad-naïve predator populations; for example, the common planigale (*Planigale maculata*; Webb et al. 2008), red-cheeked dunnart (*Sminthopsis virginiae*; Webb et al. 2011), terrestrial snake species (Phillips et al. 2003), and varanid lizards (Smith and Phillips 2006). There is also evidence that such innate avoidance may provide the raw material on which natural selection can act to generate a rapid adaptive response to toads (Phillips and Shine 2006, Smith and Phillips 2006, Llewelyn et al. 2011, Somaweera and Shine 2012, Kelly and Phillips 2017). Clearly, then, this nonbaitable fraction of the population is important, but the fraction of our nonbaitable animals that will in fact avoid toads (rather than baits) remains an important avenue for future work.

Our analysis also gives us insight into an optimal baiting rate. We explicitly modelled a link between bait availability and bait uptake probability, an effect that has been demonstrated in lethal baiting programs (Christensen et al. 2013). Interestingly, some studies suggest that low bait availability can reveal further population heterogeneity. In foxes (*Vulpes vulpes*), it is the dominant individuals that access baits first, consequently reducing access to baits for other individuals within the population (Marks and Bloomfield 1999, Gentle et al. 2004). Our findings suggest that suboptimal baiting rates can be avoided in our case by increasing baiting density to a minimum of 72 baits/site, resulting in a very high probability of bait take by the baitable fraction of northern quolls. We note, however, that our model treats per-bait encounter rate as independent of bait density. Although this is a reasonable simplifying assumption (and necessary given we did not impose variation in bait density across sites), where there is competition for baits we might well expect per-bait encounter probabilities to increase with increasing bait density as, for example, dominant individuals are removed from the competition.

Our analysis also gives us insight into the density of quolls and how this varies within the landscape. Baiting at a rate of 1 bait/ha in the northern Kimberley, and assuming an average population density, managers may reasonably expect bait uptake from only approximately 18% of the northern quoll population. Why such a low percentage? At a density of 1 bait/hectare, many quolls are simply not encountering the bait or arriving at the bait station after baits have been taken or become unpalatable. Deploying 72 baits, however, can be expected to treat almost all of the baitable quolls at a site because encounter probabilities become high enough that most individuals will encounter a bait on the night of deployment. Our parameters (bait survival and encounter rate) can also allow managers to optimize their efforts using

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not only bait density, but also bait survival. Bait density is clearly the simplest variable to adjust, but in other systems it may also be possible (and possibly more efficient) to adjust bait longevity as well.

An alternative strategy is to bait with a lower bait density, but on multiple occasions. Here, cost considerations suggest that increasing bait density (rather than number of sessions) may often be the optimal strategy. As with many programs, the majority cost associated with our baiting program is transport (helicopter time in our case). Three separate baiting occasions would result in a 3-fold increase in transport costs. On the other hand, increasing bait density would generate only a moderate increase in cost (associated with bait production). Increasing baiting density generates an increase in bait production cost, but this is a cost increase whether baits are delivered on one occasion, or 2. Alternatively, for a fixed budget, increasing bait density reduces the area that can be completely treated. Clearly, then, given a fixed budget, the optimal baiting strategy in our case will depend upon a trade-off: are we better off to treat a larger area (but fewer animals per area), or a smaller area (but treat almost all the baitable animals in that area)? This is not a trivial problem to solve and requires application of spatially explicit population viability analysis.

Multiple deployments may, however, have other advantages, not captured in cost. For example in our case, training only once prior to toad arrival will need to be delicately timed; too early, and trained animals may lose their aversion before toads arrive (Indigo et al. 2018). Thus, delivering baits over 3 occasions acts as a bet-hedging strategy against the uncertainty of toad arrival time. Clearly, baiting campaigns will often need to consider such exigencies not captured in budget figures.

MANAGEMENT IMPLICATIONS

Our results provide important information for designing a baiting program for quolls in the Kimberley. Our results may be used to guide programs elsewhere, but this should only be done with caution. Many important variables change between areas. More broadly, our results speak to the importance of careful monitoring of baiting efficacy and assessing population heterogeneity in baitability. There is clear evidence that individuals vary in their food selection and behavioural tendency to accept novel food. If our analysis had not accounted for this heterogeneity, and assumed that all individuals were baitable, we may well have suggested that all individuals could be treated if only we increased our bait density 10-fold. It is increasingly feasible to gather data required informing the design of baiting programs, and models such as ours allow us to capture the key parameters of interest to managers and decision-makers.

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SUPPORTING INFORMATION Additional supporting information may be found in the online version of this article. Figure S1. Frequency of visits to CTA bait stations by each species.

FIGURES;

Figure 1. Location of the 11 study sites (s1 to s11) and broader study area within Australian Wildlife Conservancy’s Charnley River–Artesian Range Wildlife Sanctuary, in the Kimberley region, Western Australia; ($16^{\circ}24'S$, $125^{\circ}30'E$) a 300,000 ha property managed for conservation. Study was conducted 07/19/2019–07/26/2019, sites were selected based on the detection of quolls in the Australian Wildlife Conservancy’s fauna surveys (J. Smith, Australian Wildlife Conservancy, unpublished data). Each site was separated by ≥ 5 km to maximize independence between sites.

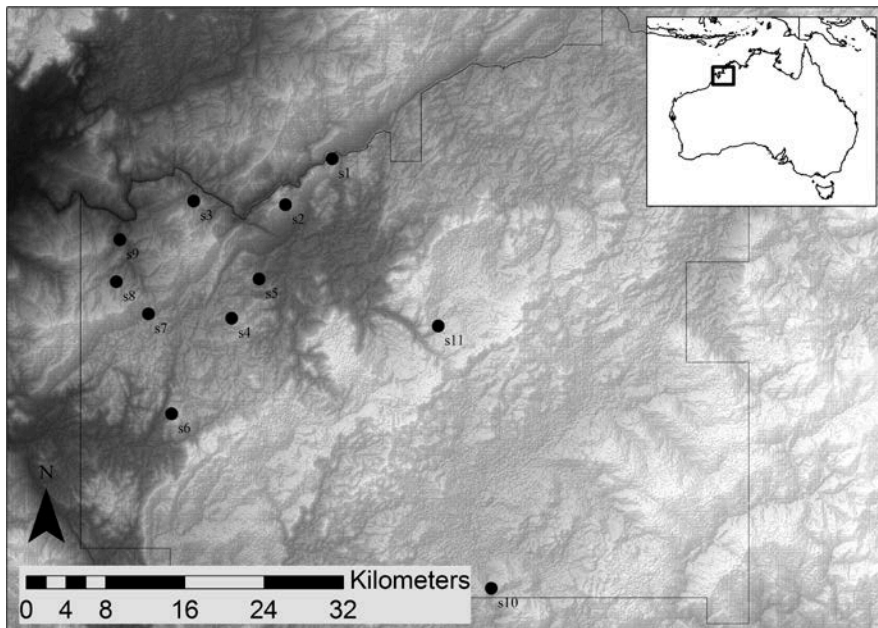


Figure 2. The Bayesian model employed for analysis summarized by a Directed Acyclic Graph (DAG) representing relationships (arrows) between the observed data and unknown parameters or hypotheses of the model (nodes). The arrows represent the relations and hierarchy between nodes. The square nodes symbolize data observed in our first and second baiting events: whether and individual at site j was observed or not at time t (within the first time period), $O_{i(j),t}$; and whether an individual was observed to take a bait at time t (within the second time period) $T_{i(j),t}$. Parameters μ_d

and β set the detection probability (d_t) driven by attraction to baited stations, and ω_j estimates the proportion of our augmented data set that represents real individuals in the population (real or not indicated by latent variable R_i). Our second baiting event—in which we deployed toad-sausage baits—was used to estimate the proportion of the population that took baits. Here, the probability of an individual quoll taking bait $u_{i,t}$ is conditional on the quoll being a ‘real’ individual $R_i = 1$, and also being initially susceptible to baiting $Z_i = 1$. The time-dependence of $u(t)$ results from 2 processes: 1) number of baits remaining at time t (B_t , determined by s); and 2) probability that an individual has already encountered a bait, has learned, and so is no longer susceptible (determined by the encounter rate, τ).

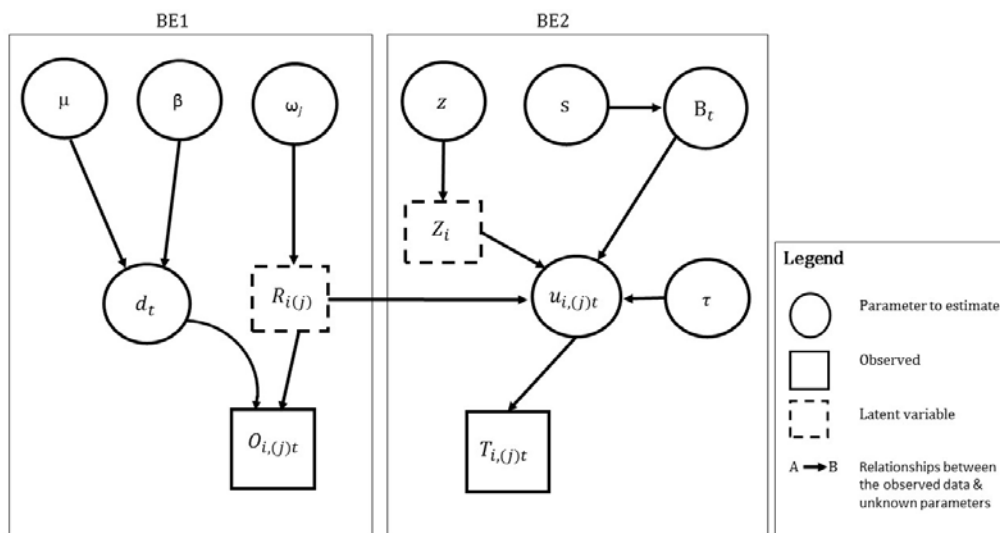


Figure 3. We compared our Bayesian modelled output with an identical model, in which we substituted a minimally informative prior for z (probability of an individual being bait-susceptible). Posterior density distribution of z when z = minimally informed prior (dashed grey line), versus when z = informed prior (solid black line).

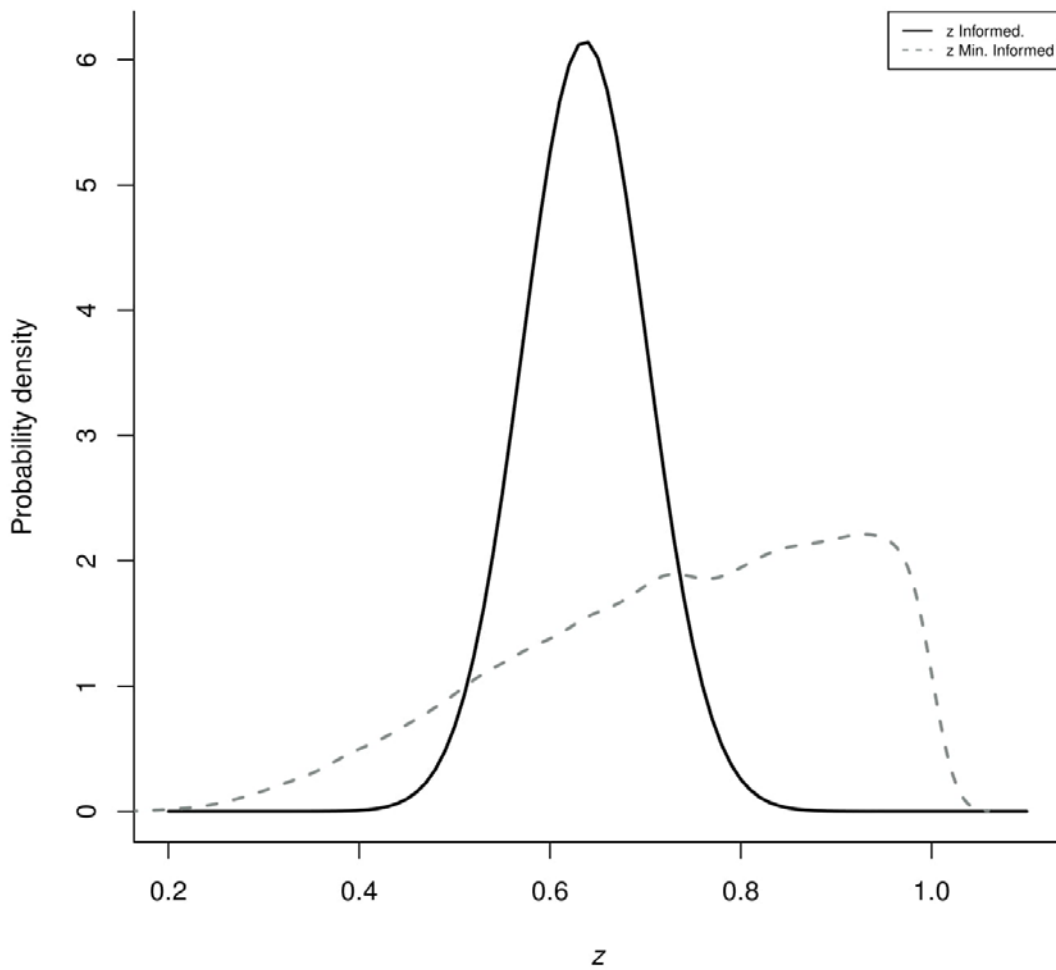


Figure 4. Parameters for bait survival and uptake probability indicated that baiting at the rate of 72 baits/7-ha site (i.e., 6 times more baits than we used) should result in essentially all baitable individuals taking bait within 5 days of bait deployment. By contrast, if we assume that all individuals are baitable, our model suggests we would need to deploy >120 baits (10 times more than we used). Figure represents modelled

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probability of bait take ($u_{i,t}$) given an individual is bait susceptible ($Z_i = 1$). Curves show uptake probability over time (days since bait deployment) comparing 2 models, in which there is heterogeneity in baitability (a: $z \sim 0.64$) and no heterogeneity (b: $z = 1$). Series on each plot represent different initial bait density.

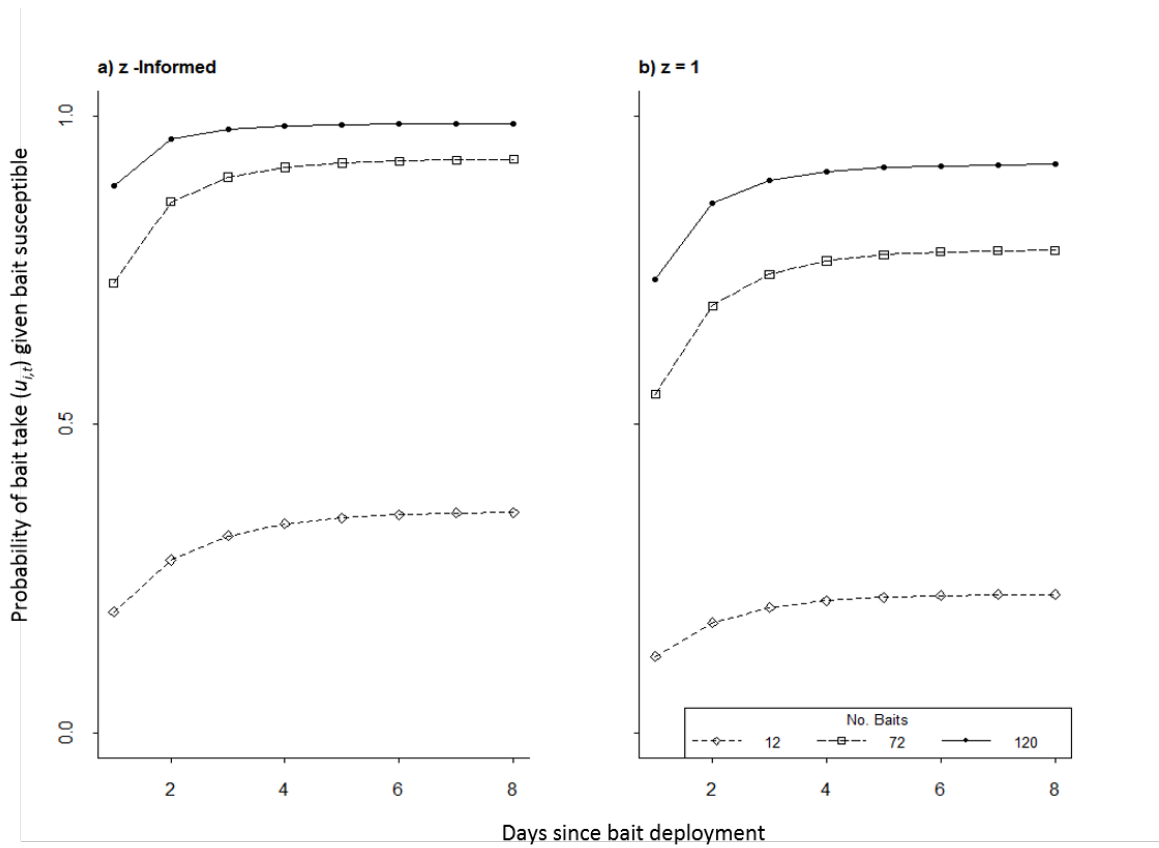


Table 1. In our Bayesian model, we used minimally informative priors except for z . For this parameter, we had prior information on the proportion of quolls likely to take a bait from Indigo et al. (2018). Bayesian model parameters and their priors including prior distributions, standard deviation, estimated posterior means and their 95% credible intervals. N denotes normal probability distribution, U denotes uniform probability distribution.

Parameter description	Parameter	Distribution (Priors, SD)	Posterior mean	95% CI
Probability of being baitable	z	N (0.63–0.064)	0.64	0.52–0.77
Intercept for detection (logit)	μ_d	N (0–1,000)	0.40	0.30–0.50
Slope of time effect on detection (logit)	β_d	N (0–1,000)	–0.20	–0.400 to –0.005
Probability of bait being encountered by an individual	τ	U (0–1)	0.018	0.009– 0.030
Per-day survival probability of bait	s	U (0–1)	0.52	0.29–0.78

Table 2. Cameras at bait stations detected 86 individual quolls across our 11 study sites. During BE2 (in which sausages were deployed), bait stations were visited by 45 individual quolls. Of these 45 individuals, 21 encountered a cane toad sausage with the remaining 24 animals arriving at the bait station after baits had been taken by other species or other quolls. Of these 21 CTA bait-exposed individuals, 18 individuals took the bait. Modelled Bayesian mark and recapture estimated population size, observed bait take for each population of quolls and the number of baits taken by nontarget species from a total of 12 baits provided per site. Posterior mean population sizes (N_j [Site 1: Site 11; Fig. 1]) and 95% credible intervals, assuming closure of the population during the time of the study (07/19/2019-07/26/2019).

Site	N_j (95% CI)	Baits taken by quolls	Baits taken by nontarget spp.
1	6.12 (5,9)	1	1
2	12.07 (10,16)	2	4
3	16.84 (14,22)	1	3
4	2.57 (2,5)	2	4
5	7.31 (6,10)	2	2
6	15.63 (13,20)	2	0
7	7.31 (6,10)	3	2
8	8.50 (7,12)	1	0
9	8.50 (7,12)	2	1

10	0.00 (0,0)	0	0
11	3.74 (3,6)	2	6

ARTICLE SUMMARY FOR TABLE OF CONTENTS:

We assess conditioned taste aversion baiting as a practical and viable management tool; by optimising bait delivery and determining the fewest baits required to achieve a given proportion of the population baited. Our results speak to the importance of careful monitoring of baiting efficacy and assessing population heterogeneity in baitability as there is clear evidence that individuals vary in their food selection and behavioural tendency to accept novel food.