TITLE: Optimising management strategies for invasive predator control: A modelling approach

**AUTHORS** (in alphabetical order):

|  |  |  |  |
| --- | --- | --- | --- |
| **Name** | **Institution** | **Adress** | **ORCID ID** |
| Rachelle N Binny | Manaaki Whenua – Landcare Research | Lincoln | 0000-0002-3433-0417 |
| Patrick M Garvey | Manaaki Whenua – Landcare Research | Lincoln | 0000-0002-6353-2624 |
| Andrew M Gormley | Manaaki Whenua – Landcare Research | Lincoln | 0000-0001-9833-7012 |
| Graham J Hickling | Manaaki Whenua – Landcare Research | Lincoln | 0000-0002-1894-7505 |
| Michael J Plank | University of Canterbury | Christchurch | 0000-0002-7539-3465 |
| Giorgia Vattiato\* | Manaaki Whenua – Landcare Research | Lincoln | 0000-0002-7994-7541 |

**\*** corresponding author, [vattiatogi@landcareresearch.co.nz](mailto:vattiatogi@landcareresearch.co.nz)

## Abstract

(1) Invasive predators pose a serious threat to native biodiversity, with trapping being one of several methods developed to manage and monitor their populations. Many individuals in these predator populations have been found to display trap-shyness, which hinders eradication and results in inaccurate estimates of population size. Lures are used to help overcome trap-shyness by increasing the probability of interaction with the device but the extent of this behavioural trait in wild populations, and the best timing for the introduction of a new lure or combination of lures, are uncertain. A key challenge for wildlife managers is maximising the efficacy of invasive predator control, particularly in relation to baiting and trapping, so that pests are extirpated, or survivors are reduced to a minimum. (2) We first use a Bayesian estimation method to quantify the trap-shyness trait in a population of brushtail possum in a New Zealand forest; the resulting estimated parameters are then used to calibrate a stochastic, individual-based model simulating the outcomes of different luring scenarios. (3) We show that the brushtail possum (*Trichosurus vulpecula*) population analysed was likely split into a smaller, very trappable group, and a larger trap-shy group, with low mean nightly probability of interaction with traps of 28% [14%-56%]. (4) Synthesis and applications: Our results show that using multiple lures can result in a greater population knock-down than using a single lure, and that it is more efficient to use a combination of lures for the entire duration of a kill-trap operation than to switch from one lure to another.

**Keywords**: pest eradication, kill-traps, lure change, trap-shyness, invasive species

## Introduction

Many of the world’s ecosystems experience a threat to their native biodiversity by invasive predator species (Bellard et al., 2016; Doherty et al., 2016; Szabo et al., 2012). Native animal populations often did not evolve with defensive skills and mechanisms required to survive encounters with these invasive predators, which makes their populations vulnerable to damage or extinction. Invasive predators have contributed to 58% of all bird, reptile, with endemic island faunas most at risk of extinction (Doherty et al., 2016). In addition to negative impacts on biodiversity, some invasive predators are vectors of diseases such as bovine tuberculosis, which can have devastating impacts on the agricultural industry and human health.

Control and surveillance of invasive mammalian predator populations are undertaken worldwide using monitoring devices, poisonous baits, and kill-traps, intended to knock-down their populations to safe levels or, in best-case scenarios, to eradicate them. Successful eradications have been achieved on islands, eco-sanctuaries, and other isolated or fenced areas but are rare in large mainland habitats. Mainland areas typically require continuous control and monitoring to avoid population recovery arising from surviving or immigrating animals.

Eradicating invasive populations is made particularly challenging by some individual animals’ recalcitrance in interacting with monitoring or control devices, a phenomenon often referred to as “trap-shyness” (Johnstone, 2021; Linhart et al., 2012; Thompson, 1953) Individual characteristics of a pest population, such as those related to personalities, demographic factors, or body condition, can contribute to trap-shyness. Animal personality has recently emerged as an important concept in behavioural ecology (Merrick & Koprowski, 2017; Réale et al., 2007) and personality has been shown to influence characteristics that are important in a pest management context such as dietary preferences (Mella et al., 2015), reproduction (Réale et al., 2000), dispersal (Bremner‐Harrison et al., 2006), and risk-taking behaviours (Mella et al., 2015). Kill-trapping selects for trap-shy survivors, which may lead to an increasingly recalcitrant population (Johnstone et al., 2023; Seymour et al., 2005; Vattiato et al., 2021). Determining the actual distribution of recalcitrant traits within a pest population is challenging and a range of scenarios are typically modelled to explore different possible personalities distributions (Vattiato, 2021). Pest managers could improve the outcomes of trapping operations by explicit consideration of individual variability, such as recalcitrant traits and dietary preferences, and alter their trapping and baiting regimes to enhance the effectiveness of pest management (Garvey et al., 2020).

Trap-shyness can potentially be overcome by the use of lures (e.g. (Clapperton et al., 2017; Garvey et al., 2017). In addition, there is evidence of different individuals preferring one lure over another, which suggests that a combination of lures might be able to target a wider proportion of the population and be the most efficient strategy for achieving eradication in kill-trapping control programmes. The probability that an individual will interreact with a trap is a product of the animal’s intrinsic fear of the device, the value of the lure to the animal, and the animal’s missed opportunity cost (MOC) (Garvey et al., 2020). Variations in MOC can alter an individual’s susceptibility to capture (e.g., a food lure when prey resources are limited), while applying more attractive lures can overcome reluctance to engage due to fear of devices. While highly attractive lures may attract most pests in a population, variation in individual dietary preferences suggests that no single lure will target all animals. Indeed, the value of a lure may change for the same individual over time (e.g., oestrous female odour during the breeding season), so that individuals exhibit variation in trappability through time (Rhoades et al., 2018).

In this paper, we use a spatially explicit, individual-based model to simulate the dynamics of a behaviourally heterogeneous predator population during a kill-trap eradication program. We use a simple Bayesian inference method to calibrate key model parameters associated with heterogeneity in trap-shyness, by fitting the model’s predicted number of captures over time to a dataset of possum captures in a New Zealand forest. We then use the calibrated model to predict how different combinations of lures targeting the trap-shy individuals in the population will affect its knock-down success.

## Methods

We use a stochastic, individual-based model including density-dependent reproduction, mortality, and density-dependent home-range radii, similar to that described in Vattiato (2021). We calibrate the model using data from a pest removal experiment conducted using kill-traps to remove invasive brushtail possums (*Trichosurus vulpecula*) from a New Zealand conservation reserve where the overabundant possum population was impacting native species biodiversity.

*Study area and trap grid*

The trapping experiment is described in detail in Johnstone et al. (2023). Briefly, possums were trapped from the Lottery Bush 120 ha reserve of old-growth beech/podocarp forest that was fenced to exclude livestock that grazed on surrounding pastures. Prior to the experiment, there had been no significant trapping in the reserve in recent years, with possum sign found throughout the reserve at levels suggesting posum abundance was near the ecological carrying capacity of the habitat.

In early May 2021, 66 possum kill-traps were installed on transects within the reserve (Figure S1). These transects followed forest margins, ridgelines, and other landscape features expected to favour possum movement and trap encounters. Traps were attached to tree trunks c. 50 cm above ground level (Figure 1). Possums that inserted their head through an opening in the trap to access bait triggered a lethal kill-bar. Traps were baited with peanut butter placed on the trigger mechanism and lured with mixture of flour and icing sugar smeared on the tree trunk below the trap. The traps were not self-resetting, so regular visits by field staff were required to clear carcasses and re-set sprung traps.

***A raccoon on a tree

Description automatically generated***

**Figure 1**. Example of a brushtail possum interacting with a Sentinel® kill-trap deployed in the forest reserve.

Additional kill-traps were deployed in June and July 2021, resulting in the eventual deployment of 105 active traps across the entire reserve (Figure S1). The expected home range of possums in eastern forest habitat is c. 1–2 ha (Cowan and Glen 1990), so this trap coverage provided high confidence that all possums within the reserve would have at least one kill-trap within their home-range. Initially, traps were checked and reset twice a week. As possum numbers declined and catch rates fell, the interval between checks lengthened progressively. Johnstone et al. (2023) reported on catches up until January 2021; trapping continued for several years thereafter.

The reduction in possum abundance in the reserve achieved by kill-trapping was assessed using several indices of relative possum abundance. Kill-trap catch rate was monitored but it was recognized that trap-shyness would increasingly bias this rate. Therefore, trail camera and chew-card surveys were also implemented prior to the start of trapping and again in June and in September 2021. Capture rates for cage traps and padded leg-hold traps used to sample live possums from the reserve were also recorded. Collectively, these several indices were consistent in suggesting that possum numbers in the reserve had been substantially reduced by October 2021 (see Table 1 in Johnstone et al. 2023).

In the model described below, the study area was simplified to a 175 ha rectangle encompassing the trap layout, with a 100m buffer from the outermost traps in each direction. Simulated possum home-ranges were randomly placed within this rectangle.

**Density-dependent reproduction and natural mortality**

Possum populations show density-dependent effects on fecundity (Cowan & Glen, 2021; Ramsey et al., 2002). We model the birth rate at time as

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| --- | --- |
|  | (1) |

Where is the per-capita annual birth rate in the low-density limit, is a coefficient representing the strength of density-dependent effects on birth rate (see below), and corresponds to the normal probability density function used to model the reproduction season, evaluated at day , and truncated to [0, 365] days. To account for the gestation period, we update the density dependent term by using the number of live adults at time , the beginning of the reproduction season, estimated at the 1st of February (Table 1).

Brushtail possums in New Zealand have been observed to have one major breeding season starting at the end of summer and lasting for 3-4 months (Cowan & Glen, 2021; Crawley, 1973; Lustig et al., 2019). A small portion of females have a second breeding season in spring. For simplicity, we ignored the second breeding season and modelled reproduction season as a normal distribution centred around the 1st of April and with a 20-day standard deviation (Table 1). Note that we include reproduction in our model for generality, but our simulations are limited to an eight-month period starting immediately after the end of a breeding season, hence reproduction will have a negligible effect on population dynamics in the scenarios presented in this paper.

Natural mortality is modelled as a constant per capita mortality rate per unit time using the formula

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|  | (2) |

with being average life expectancy.

The expected number of newborns and natural deaths on a given day is then calculated as

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| --- | --- |
|  | (3) |
|  | (4) |

where =1 day is the time step.

Newborns do not affect the density-dependent fecundity until they are one year of age, but they can die naturally or from trapping at the same rates as adults.

Note that in the absence of trapping the model behaves like a stochastic density-dependent individual-based model with seasonal reproduction (Supp. Figure S3, top). The population size will be at statistical equilibrium when . This implies that the value of the coefficient must equal where is the size of the study area and is the carrying capacity for population density.

The study area for the model fitting simulations is given an arbitrary value of 175 ha (Table 1). The carrying capacity possums ha-1 is taken from the values allocated to New Zealand land cover classes by Warburton et al. (2009), corresponding to a non-controlled population of possums in a mixed beech-podocarp-broadleaved forest. The value of is set by noting that is the net rate of per capita population growth in the low-density limit, a quantity for which estimates are available in the literature for brushtail possums in New Zealand (Cowan & Glen, 2021).

**Probability of capture**

The probability of an animal being captured or detected by a device is partitioned into two components: the probability that the animal encounters a device within its home-range area, and the probability that it interacts with and triggers that device given an encounter. For brushtail possum, the probability of an animal encountering a device is inversely related to its home-range size (Ball et al., 2005). This relationship depends on several factors including the trap grid spacing, the animal’s denning behaviour, movement rate and perception distance (Vattiato, 2021). For the model fitting procedure, we use the same trap grid layout as the one used in the field trial (Johnstone et al., 2023). For the scenario simulations, we use a generic homogeneous landscape of fixed area ha overlaid with a square grid of traps with distance m between traps (Table 1).

We define the nightly capture probability by one device , i.e. the probability that an individual encounters and triggers a device set at a distance from its home-range centre, in a single night, as

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| --- | --- |
|  | (5) |

where is the probability that the individual encounters a device at distance from its home-range centre, and is the probability that the individual interacts with the device, given encounter. We model population heterogeneity at the individual level, by assigning a different probability of interaction to each individual in the population, with each value drawn from a Beta distribution with mean and variance . We infer these last two parameters by fitting our simulation model to capture data, as described in the next section.

The value of the probability of encountering a single trap at a distance from the home range centre is not well described in the literature. However, we can derive it from Equation (5) and the well-established relationship (Efford et al., 2009) as:

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| --- | --- |
|  | (6) |

where is the average nightly probability of capture at the home-range centre (i.e. ). Ideally, we would have a measure of for each individual in a population, to account for individual differences in trappability. However, as estimates of reported in the literature do not distinguish between individuals, we assume in Equation (5) to derive Equation (6), with being the mean of the distribution of initial values for our simulated population, prior to control (Table 1). The spatial-decay parameter is a measure of the individual’s home-range size: assuming an animal occupies its home-range, on average, according to a symmetric bivariate normal distribution, then the area the animal occupies 95% of the time is a circle of radius with area (Efford, 2004; Efford et al., 2004). Estimates of and can be obtained by fitting spatially explicit capture-recapture (SECR) models to capture-recapture data (Borchers & Efford, 2008; Efford & Fewster, 2013), and estimates for brushtail possum populations have been reported for a range of population densities and different environmental conditions (Vattiato et al., 2023) . For brushtail possums there is an inverse relationship between (and therefore ) and (Anderson et al., 2021; Sweetapple & Nugent, 2018; Vattiato et al., 2023), resulting from animals with larger home-range areas spending, on average, less time at the home-range centre than animals with a smaller home-range, and which for brushtail possums in New Zealand is best described by the power law for each individual , with (Vattiato et al., 2023). See Supp. Figure S2 for some graphical examples of the relationship between and . There is also an inverse relationship between and population density of possums (Anderson et al., 2021; Efford et al., 2016), best described by the function , with (Vattiato et al., 2023).

At the beginning of each simulation, the coordinates of each animal's home-range centre are randomly drawn from an array of possible locations. This position is used to calculate the distance to each trap located within the home-range area of individual and the associated probability of the animal encountering trap in a single night using Equation (6). The probability that individual encounters at least one of the traps in its home range in a single night is then calculated as follows:

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| --- | --- |
|  | (7) |

where is the total number of traps in the home-range. These calculations are done independently for each individual, and while the randomly drawn home-range centres can result in an overlap of home-ranges, we assume that each animal's is not affected by the position of other animals’ home-ranges. Supp. Figure S3 illustrates how an increase in population size corresponds to a decrease in average home-range radius, and consequently a decrease in the population’s average total probability of encounter .

**Parameter inference and ABC model fitting**

We use an approximate Bayesian computation (ABC) approach to fit the model to field data and estimate three of the model parameters: the mean and variance of the Beta distribution from which the individual values were drawn at the start of the simulation, and the initial population size , with prior distributions defined in Table 1. We fit the modelled number of captures, corresponding to the total captures in the time periods between each check of the traps, to observed number of captures from data collected at Lottery Bush (Johnstone et al., 2023). The prior distributions chosen for the two parameters relating to the distribution were wide and uninformed (see Table 1), as there is little to no information on the distribution of individual interaction probabilities in wild possum populations. The prior chosen for the initial population size was left-bounded with the total number of captures from the Lottery Bush data, and right-bounded with double that number of captures. This assumes that at least 50% of the Lottery Bush population was caught by the end of the trapping operation, which is a reasonable assumption considering the large reduction seen in multiple indices of possums’ relative abundance (Johnstone et al., 2023).

For each combination of parameter values, randomly drawn from their prior distribution, we run the model and calculate an error function, defined as

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|  | (8) |

With being the timestamps of the available capture data, being the modelled captures at time and being the observed captures at time . We ran the model for 30,000 parameter combinations and retained the 300 combinations corresponding to the 1% smallest errors to produce an approximate posterior distribution.

**Change of lure scenarios**

To explore the effect of using different combinations of lures, and different timings for the change to a new lure on the success of a trapping operation, we simulated seven different scenarios, with two different catch rate thresholds (i.e., the ratio of the current catch rate over the initial catch rate that triggered a change in lure), as defined below, and two kinds of “new lure” (Table 1). We ran 10,000 simulations for each scenario using parameter values drawn from the posterior. For each scenario, we then reported the median and 95% credible intervals for the final population size and the mean of the final population.

The baseline scenario corresponds to one where we keep applying the default lure (lure A) for the entire duration of the trapping programme. Individuals’ values for interaction with lure A are randomly drawn from the best fitting distribution obtained through the ABC model fitting, and they remain constant until the end of the simulation.

For the lure combination scenarios, we draw two independent values of for each individual, one for lure A, and one for the “new lure”. The independence of the two values is an arbitrary modelling choice corresponding to a best-case scenario. At each time step, individuals have some probability of encountering a trap with either of the two lures, dependent on the lure combination layout (described in the next paragraph), and a lure-dependent probability of capture given by , with being the probability of interaction assigned to individual for lure . Note that the values for each lure are drawn independently from each other, which means that an individual could be very trap-shy towards lure A, but very attracted towards the second lure, and vice versa. In other words. B is simulated to have the same average attractiveness as lure A, but will attract a different subset of the population. This approach accounts for individual preferences and variation in risk-taking behaviour.

We also tested two different “new lures” (called B and C), one corresponding to a distribution of identical to that for lure A (beta distribution with mean , standard deviation ), and a more attractive one corresponding to a distribution of with mean 2 and standard deviation , i.e. double the mean and equal variance of that for lure A.

We considered two different luring scenarios: one where the two lures (default and new) are present in equal numbers for the entire duration of the programme (each individual has a 50% probability of encountering either on any night), and one where all lures are switched from the default to the new lure once the ratio of the current daily catch rate (averaged over the past seven days to correspond with standard trapping practice) over the initial daily catch rate drops by a set amount (Table 1). Note that for the scenario where both lures are present concurrently, we do not explicitly model the position of each lure. Instead, for simplicity, we assume that when an individual encounters a trap, it contains the default lure with probability 0.5 and the new lure with probability 0.5, independent of previously encountered lures.

Table 1 - Parameter values used in the population dynamics simulations for the exploration of the effects of trap-shyness on pest eradication.

| **Parameters** | **Symbol** | **Value** | **Comments/references** |
| --- | --- | --- | --- |
| LANDSCAPE |  |  |  |
| Study area | *A* | 175 ha | Model fitting simulations use A=1160m x 1660m to encompass trap layout from (Johnstone et al., 2023) |
| Square trap grid spacing |  | 100 m | Model fitting simulations use the same trap layout as in (Johnstone et al., 2023) |
| Carrying capacity | *K* | 9 possums ha-1 | (Warburton et al., 2009), value corresponding to populations of possum in New Zealand’s mixed beech-podocarp-broadleaved forests |
| POPULATION |  |  |  |
| Trap perception distance |  | 10 m | Assumed |
| Lifespan in the absence of control measures |  | 13 yrs. | (Cowan, 2001) |
| Annual birth rate |  | 0.77 | Calculated as annual growth rate in Cowan and Glen (2021) + annual mortality rate from Eq. (2) |
| Peak of reproduction season (mean of f(t)) |  | 1st April | Assumed |
| St. dev. of reproduction season function f(t) |  | 20 days | Assumed |
| Maximum home-range radius |  | 380 m | Corresponding to the maximum value of (155 m) found in Vattiato et al. (2023) |
| Nightly probability of capture at home-range centre |  | variable | See text in “Probability of capture” |
| Home-range spatial decay parameter |  | variable | See text in “Probability of capture” |
| Initial mean of default population’s beta distribution |  |  | Fitted |
| Initial variance of default population’s beta distribution |  |  | Fitted |
| Initial population size |  |  | Fitted |
| CHANGE OF LURE SCENARIOS |  |  |  |
| Catch rate threshold |  | [80%, 95%] |  |
| Initial mean of population’s beta distribution for lure |  |  |  |
| Initial mean of population’s beta distribution for lure |  |  |  |
| SIMULATIONS |  |  |  |
| Time step | *dt* | 1 day |  |
| First day of trapping |  | 1st June |  |
| Last day of trapping |  | 31st January |  |

## Results

**Model fitting**

The simulation model resulted in a reasonable fit to the Lottery Bush capture data (Supp. Figure S4). The marginal posterior distributions for the mean and variance parameters of the beta distribution for the initial population’s had median and 95% credible interval values [0.14, 0.56] and [0.04, 0.20]. Both these sets of parameter values correspond to a “U-shaped” Beta distribution for the probability of interaction (Figure 1d), meaning that most individuals in the initial population had interaction probabilities that were either very low (“trap-shy” individuals) or very high (“trappable” individuals). A comparison of model results and fitted data can be found in Supp. Figure S4.

The marginal posterior distribution for the initial population size had a median and 95% credible interval values of [141, 268], the distribution was strongly left-skewed (Figure 2c), indicating that most of the population had been caught during the trapping operation at Lottery Bush.

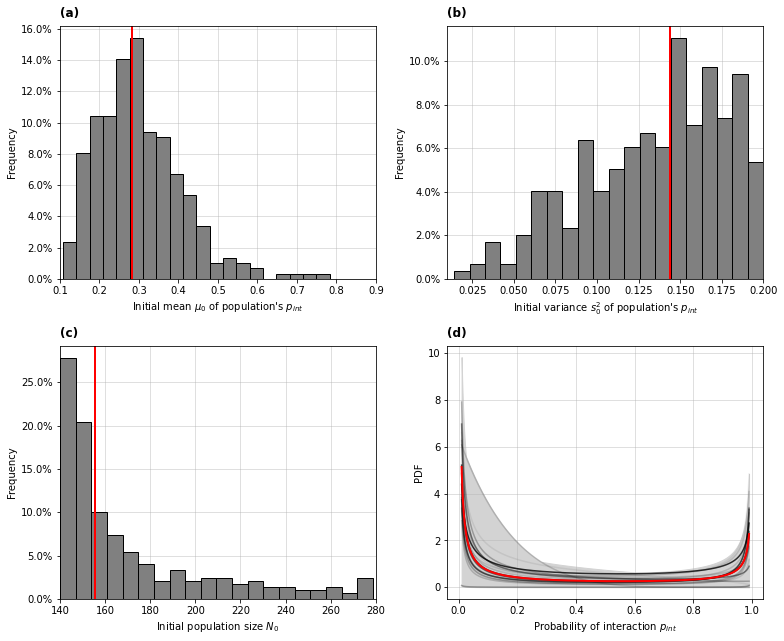


Figure 2 – Histograms showing the marginal posterior distributions of each of the three fitted parameter (a, b, c) for the 300 accepted model runs (1% best runs resulting from 30,000 random draws from the prior (Table 1)), with the best fitting parameter set indicated in red. (d) Posterior Beta distributions, including the distribution function corresponding to the median and (red line), used to randomly draw the individuals’ probabilities of interaction at the beginning of each scenario simulation, a credible interval enveloping the distributions corresponding to the 1% best fitting parameter sets (grey shaded area), and a sample of 20 posterior beta distribution functions (grey lines, with a transparency gradient which reflect the goodness of fit of the corresponding posterior parameter set - the darker the line, the smaller the associated error).

**Scenario runs**

Using the 300 posterior parameter sets from the ABC model fitting, we ran 10,000 simulations for each of the seven scenarios (six lure combinations and one single-lure baseline) described in the methods. Each simulation was run using a randomly drawn parameter set from the 300 accepted sets. Results (Table 2) show a significant additional reduction in the surviving population after eight months of trapping for all combination-lure scenarios compared to the reduction achieved by the single-lure baseline. Within the combination lure scenarios, those that had both lures for the entire duration of the programme resulted in the highest reduction in population size after eight months. As expected, using a lure corresponding to a distribution of with double the mean as that of the default lure produced to the strongest effect, with only 5% of the initial population left uncaptured after eight months. Supp. Table S1 also shows a summary of the timing when the most trappable individuals have been caught and daily captures plateau, with the combination lure scenarios plateauing slightly later than the single lure one, but at much lower population numbers. All simulated scenarios resulted in a very low mean probability of interaction given encounter in the surviving population.

Table 2 – Final population and mean with lure A of the final population after eight months of trapping, for both the baseline scenario and each combination lure scenario. Results show the median over 10,000 simulation repetitions and the 95% credible intervals.

|  |  |  |
| --- | --- | --- |
| Scenario | Surviving population | Mean towards lure A of surviving population ( |
| *Lure A (baseline)* | 50 [10, 152] | 0.0008 [0.0001, 0.0029] |
| *Lure A + B from* | 21 [1, 106] | 0.0012 [0.0000, 0.0074] |
| *Lure A until , then lure B  (low change threshold – 80% drop in daily captures)* | 29 [3, 118] | 0.0230 [0.0005, 0.0888] |
|  |  |
| *Lure A until , then lure B  (high change threshold – 95% drop in daily captures)* | 26 [2, 114] | 0.0134 [0.0005, 0.0575] |
|  |  |
| *Lure A + C from* | 7 [1, 50] | 0.0009 [0.0000, 0.0210] |
| *Lure A until , then lure C  (low change threshold – 80% drop in daily captures)* | 8 [1, 52] | 0.0165 [0.0000, 0.1336] |
|  |  |
| *Lure A until , then lure C  (high change threshold – 95% drop in daily captures)* | 7 [1, 55] | 0.0101 [0.0000, 0.0817] |
|  |  |

## Discussion

We have used a spatially explicit model of population dynamics during a kill-trapping operation, fitted to a brushtail possum capture dataset from a New Zealand forest reserve, to estimate the population’s distribution of the trap-shyness trait. Our model-fitting results indicated that the possum population in the reserve was mostly comprised of a group of highly trap-shy individuals and a slightly smaller group of highly trappable ones. Our estimates of the initial population size suggested that most of the population had been caught by the end of the four-month long trapping operation.

We then ran several scenarios considering different combinations of lures and different timings for the introduction of a second lure, using with the best-case scenario assumption that animals’ reactions to different lures are independent. All these scenarios resulted in a very low mean probability of interaction given encounter in the surviving population, which highlights the vexing problem that pest managers face – that the surviving animals left at the end of a trapping operation are typically the most trap-shy individuals. Our results also suggested that having a mix of both lures for the entire duration of the trapping operation is more effective than switching from one lure to another part way through the operation. Regardless of the lure combination used, there will still be some very trap-shy individuals that remain uncaught. These last trap-shy individuals may be able to be targeted in several ways, depending on our assumptions on their behaviour. If we assume that individual trap-shyness towards a specific lure is completely independent from their trap-shyness towards other lures, the best strategy would be to keep introducing additional lures to try and cater to every individual taste. However, if animals’ trap-shyness is somewhat independent of the lure used, introducing additional lures will have no effect on the surviving population, which will have to be eradicated using more intensive methods. Real-world populations probably display a combination of these factors: introducing a new lure will catch some of the remaining survivors, but some of the most trap-shy individuals will remain free. The ideal management strategy would be to use lured traps to reduce the population to the last trap-shy individuals, and to then use other devices (such as camouflaged leg-hold traps or dogs), whose efficacy is independent of the possums’ kill-trap response.

The model described in this paper was a useful tool to explore different scenarios of lure combinations, however, it has some important limitations that need to be considered. Because of the short time frame modelled (eight months starting on 1st June), we assumed a closed population, with the only driver of population size being density-dependent reproduction. We do not model immigration from external populations or range expansion by neighbouring possums, which are known to be an important factor in longer-term eradication operations. In the scenarios with both lures present at the same time, we do not explicitly model which traps are lured with either lure type, instead we assume an equal probability of encountering a trap with either lure. This is a reasonable assumption for scenarios with only two lure types and with a high density of traps, however our results might not apply in scenarios with low trap densities or with a higher number of lure types, where lures would have to be regularly swapped between traps to ensure encounter by each individual. In addition, our assumptions on the attractiveness of the second lures were purely arbitrary, as little is known about brushtail possums’ relative levels of attraction towards different lures. Future work should focus on more field or pen trials where individual behaviour towards kill traps is repeatedly tested using different lure compounds, to justify our assumptions of a consistent individual behavioural response to a particular lure, and of independence of attraction levels towards different lures.

Our model also assumed no change in trap-shyness after a failed interaction with a trap. These events are relatively common for possums (Warburton, 1982) and other invasive predators (Weihong et al., 1999), and they can significantly increase individual trap-shyness, leading to a population more difficult to eradicate. Individuals can learn from a failed interaction with a trap: an escape from a triggering device is likely to change a possum from trappable to trap-shy. In such a scenario, alternative lures are unlikely to override the learned shyness, and changes in trap type or to passive control methods will be required.

Eradication of invasive predators is an extremely challenging goal that is rarely achieved other than on offshore islands or within predator-fenced sanctuaries, both of which block predator immigration from outside of the eradication area. Even when immigration is prevented, island and sanctuary eradications often require rapid deployment of toxic bait so that the entire predator population can be removed within a short period of time. Our modelling study, and the underpinning field data, illustrate why trapping is unlikely to achieve predator eradication unless supplemented with other control methods. Firstly, average for a widespread predator population will typically be well below 0.5, which means that even in the absence of capture heterogeneity it will take weeks or months to substantially reduce the population. This creates a ‘long tail’ effect whereby the per capita effort required to capture or kill further predators rises exponentially (see Figure 1 in Johnstone et al. 2023).

Secondly, real-word predator populations do indeed exhibit pronounced capture heterogeneity, making it even harder to capture individuals from post-control residual populations. Improved luring methods offer a potential way to address this problem; in a ‘best case’ scenario (as modelled here, with different lures operating independently in attracting different subpopulations of predators) the use of a second lure can substantially reduce – although still not eliminate – the surviving population (see Table 2). The advantage of using multiple lures will be reduced, however, if the multiple luring effects do not operate independently; that is, if the animals strongly attracted to one lure also tend to be attracted to the other lure. Currently there is almost no available data on the dependence/independence of predator’ responses to multiple lures. We suggest, however, that the best prospects for achieving an additive effect of multiple lures may come from combining lures that target different sensory modalities. For example, a lure that combines auditory, visual, and olfactory stimuli may succeed in attracting a greater number of trap-shy individuals than a lure that combines, say, three different olfactory cues. Testing this hypothesis could be a helpful next step in developing more effective multi-lure strategies for invasive predators.

## Conflict of interest

We have no conflict of interest to disclose.

## Authors contributions

All authors conceptualised the project; PG and GH provided the field data, GV produced and analysed the simulation data; GV, TB, PG, GH and MJP contributed to the interpretation of the analysed data, GV, RB, PG, GH and MJP undertook the writing, reviewing, and editing of the manuscript; All authors reviewed the results and approved the final version of the manuscript.

Our study was based on theoretical simulation, and analysis of secondary data rather than primary data. As such, there was no local data collection. All authors are based in the country where the study was carried out and were engaged early on with the study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

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## Data availability statement

The dataset used to calibrate our model is publicly available through the Manaaki Whenua Landcare Research datastore repository (DOI: <https://doi.org/10.7931/6y1w-s375>).  
The simulation model code is publicly available on the Github repository <https://github.com/Giorgia93/ShyCatchModel.git>

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