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Modelling tropical fire ant (*Solenopsis geminata*) dynamics and detection to inform an eradication project

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Abstract Invasive species threaten endangered species worldwide and substantial effort is focused on their control. Eradication projects require critical resource allocation decisions, as they affect both the likelihood of success and the overall cost. However, these complex decisions must often be made within data-poor environments. Here we develop a mathematical framework to assist in resource allocation for invasive species control projects and we apply it to the proposed eradication of the tropical fire ant (*Solenopsis geminata*) from the islands of Ashmore Reef in the Timor Sea. Our framework contains two models: a population model and a detection model. Our stochastic population model is used to predict ant abundance through time and allows us to estimate the probability of eradication. Using abundance predictions from the population model, we use the detection model to predict the probability of ant detection through time. These models inform key decisions throughout the project, which include deciding how many baiting events should take place, deciding whether to invest in detector dogs and setting surveillance effort to confirm eradication following control. We find that using a combination of insect growth regulator and toxins are required to achieve a high probability of eradication over 2 years, and we find that using two detector dogs may be more cost-effective than the use of lure deployment, provided that they are used across the life of the project. Our analysis lays a foundation for making decisions about control and detection throughout the project and provides specific advice about resource allocation.

Keywords Ashmore Reef · Eradication · Invasive species · Invertebrates · Optimal detection · Stochastic modelling · Monitoring

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Introduction

Islands are global biodiversity hotspots (Veitch and Clout 2002; Dawson et al. 2015) and are often under threat from invasive species (Courchamp et al. 2003; Gurevitch and Padilla 2004; Bellard et al. 2016). Fortunately, invasive species eradications often proceed on relatively small islands, making eradication achievable and economical (Pluess et al. 2012; Baker and Bode 2015; Holmes et al. 2015), with their isolation mitigating the threat of re-invasion (Veitch and Clout 2002). An eradication plan must consider many issues including economic, occupational health and safety, legislative requirements, and non-target impacts, as well as ultimately provide an assessment of the likelihood of eradication success (e.g. Howald et al. 2007).

Due to the limited resources available for invasive species management (McCarthy et al. 2012), it is critical that eradication programs are cost-effective. Modelling has an important role to play here, in generating predictions of the outcomes from different management actions, allowing more informed decisions (e.g. Spring and Cacho 2014). Models explicitly formalise our best knowledge of the system's dynamics and allows us to simulate these dynamics forward through time, allowing us to assess and compare different management strategies (Krug et al. 2010). This process helps make decisions more transparent and reproducible—something that conservation biologists are increasingly advocating (Gregory and Long 2009; Blomquist et al. 2010; Donlan et al. 2014).

Models have been widely implemented in various conservation biology contexts; however, modelling to assist in the early planning stages of an eradication program is uncommon. Eradications have potential for undesirable impacts, either as a direct consequence of an action (e.g. non-target mortality) or indirect, e.g. ecological change mediated by success (e.g. predator release) (Zavaleta et al. 2001; Buckley and Han 2014). When this happens, models are often developed to retrospectively identify causal factors (Courchamp et al. 1999; Bergstrom et al. 2009). Modelling has also been employed to quantify the probability of success, or alternatively, where eradication has not succeeded, to help management understand what went wrong (Ramsey et al. 2009, 2011; Rout et al. 2014a). Other types of analyses include optimising monitoring effort spatially (Hauser and McCarthy 2009; Epanchin-Niell et al. 2012; Guillera-Arroita et al. 2014), balancing quarantine, control and monitoring (Moore et al. 2010; Rout et al. 2011), and modelling to assess the best order to eradicate multiple invasive species (Raymond et al. 2011; Bode et al. 2015). With few exceptions, these approaches focus on a single aspect of an eradication project and such analyses are often completed when projects are already well progressed.

In this paper we introduce a modelling framework that can be implemented at the beginning of an eradication project to guide resource allocation and estimate project success. This modelling approach predicts species abundance and detectability, allowing us to estimate the efficacy of control efforts and compare and optimise different detection methods. We apply it to the proposed eradication of the invasive tropical fire ant (*Solenopsis geminata*) from the islands of the Ashmore Reef Commonwealth Marine Reserve in the Timor Sea. The tropical fire ant, a highly successful tramp ant native to the Americas (Fig. 1) now displays a pantropical distribution (Holway et al. 2002). First detected at Ashmore Reef in 1992 (Hodgson et al. 2014), recent work has demonstrated that, as a generalist scavenger and predator, tropical fire ants have caused seabird and turtle nest failures (Hodgson et al. 2014; Hodgson and Clarke 2014). Elsewhere tropical fire ants have impacted native invertebrate communities, soil seed banks and ecosystem functions (Holway et al. 2002; Lach and Thomas 2008; Plentovich et al. 2009). Due to the impacts, a pilot control program has been completed to assess tropical fire ant control and detection at Ashmore Reef. The aim of this study is to use available data to inform resource allocation across the project as best we can. Specifically, we seek to understand how different bait types and deployment strategies affect project success, optimise search effort when detecting remaining colonies and predict whether canine detection could be more cost effective than lure detection.

Methods

Ashmore Reef and the tropical fire ant

Ashmore Reef includes four low lying cays dominated by seasonal grasses and herbs that provide important nesting areas for seabirds and turtles (Clarke et al. 2011). The tropical fire ant has a near-continuous

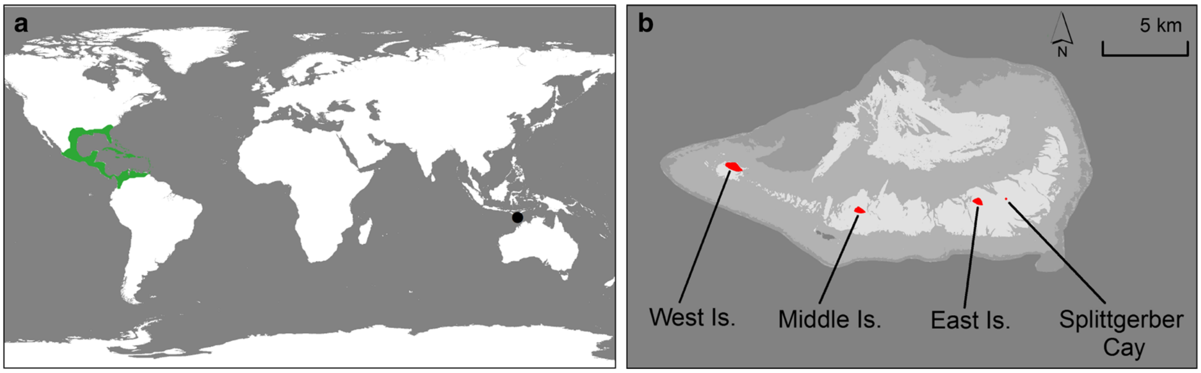

Fig. 1 **a** Indicative natural distribution of tropical fire ant (*green shading*) relative to the location of Ashmore Reef (*black circle*). **b** Ashmore Reef, showing the position and relative size of individual islands (*red shading*). All islands are occupied by tropical fire ants

distribution above the high tide line on all islands. A pilot ant control program principally involved seven discrete baiting events on Middle Island during 2011 and 2012, using both insect growth regulator (IGR) and toxin (Hodgson and Clarke 2014). Ant abundance was measured on Middle Island, using lures, on eight occasions, before, during and after treatments. We use 'ant activity'—the number of ants present on a lure after approximately 30 min—as a measure of abundance. Ideally we would keep track of the number of queens in the population, as eradication is complete only when there are no queens remaining. However, tropical fire ant colonies can have multiple queens and there is no efficient method to measure the number of queens. Hence, ant activity is the best available metric of tropical fire ant abundance in this case. The untreated East Island was monitored on four occasions during the same period. Detectability trials were also conducted to assess how frequently a lure would detect the presence of an ant colony. Eighty lure locations were established (without prior knowledge of colony location) and these were deployed and recovered each morning over six consecutive days. Any non-detection was confirmed by a visual search of the area within 10 m of the lure.

The eradication plan advises aerial baiting (delivered by helicopter) as the main suppression method for tropical fire ants. There are two bait classes under consideration: insect growth regulator (IGR) and toxin. IGRs are targeted to the tropical fire ant, but only suppress colony growth, without causing direct mortality (Hoffmann 2011). Toxins are effective at suppressing the tropical fire ant, but also affect other species. Following the baiting phase, there will be a surveillance phase, to determine if the eradication is successful. Lures are the standard method to detect tropical fire ants; however, trained detector dogs have shown promise in detecting invasive species (Brooks et al. 2003; Lin et al. 2011).

Model framework

Our framework is based around two models: a population model and a detection model (Fig. 2). The population model predicts the ant abundance in the future and the likelihood that a proposed control schedule will eradicate ants. An important part of invasive species eradications is confirming the absence of the species: the surveillance phase, which happens following the control phase. Therefore, we use a detection model to estimate the probability of detecting ants during a survey. In this monitoring phase, species can either be absent or present. If present, the population model estimates abundance, which the detection model uses to estimate the probability of detection. This allows us to calculate the probability of failing to detect the species, even though it is present (false negative). The probability of a false negative is insufficient to estimate the probability of eradication. However, using it in conjunction with a prior estimate of absence (from the population model) it allows us to quantify the probability of eradication, which we detail later.

Population model

We model tropical fire ant abundance, $n(t)$, using a stochastic difference equation:

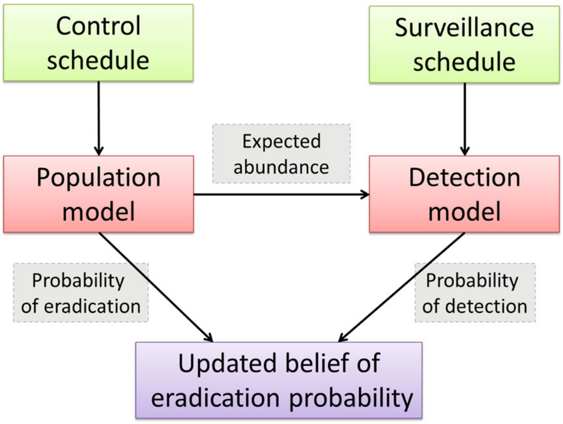

Fig. 2 A framework for optimising invasive species' eradication and detection. This framework describes how decisions about the control actions and surveillance effort are used by models to estimate the probability of eradication. The *green boxes* (control and surveillance schedules) are management decisions. Surveillance decisions would typically (but not necessarily) be delayed until the control phase is nearing completion. The *red boxes* represent models that make predictions and estimates about and of the future state of the system. The population model predicts the abundance through time and also gives an estimate of the probability of eradication. The detection model uses the abundance prediction to estimate the future ant detectability. This, combined with the surveillance schedule gives the probability that the surveillance will detect the species. Finally, this detection probability is combined with the population model's estimate of probability of eradication to give an updated belief of the probability of eradication

$$\boldsymbol{n}(\boldsymbol{t}+1) = \boldsymbol{n}(\boldsymbol{t}) + \frac{1}{52}\Big[\boldsymbol{b}(\boldsymbol{t})(1-\boldsymbol{u_{IGR}}(\boldsymbol{t}))\boldsymbol{n}(\boldsymbol{t}) - \boldsymbol{d_n}\boldsymbol{n}(\boldsymbol{t}) - \boldsymbol{u_T}(\boldsymbol{t})\boldsymbol{n}(\boldsymbol{t}) - \boldsymbol{d_{dd}}\boldsymbol{n}(\boldsymbol{t})^2 + z_t\sqrt{\boldsymbol{n}(\boldsymbol{t})}\Big], \tag{1}$$

where t is time, measured in weeks (hence the factor of 1/52, as each of the other rate parameters are in years). The first term is the population growth rate, influenced by the birth rate, $b(t)$, and the effect of insect growth regulators, $u_{IGR}(t)$, which takes values between 0 and 1. The second term is the natural death rate, d_n. The third term is the rate of decline of ant abundance due to the effect of toxin, $u_T(t)$. The fourth term models the effect of density dependence through the parameter d_{dd}, and the fifth term models demographic stochasticity through z_t, which is a normally distributed random variable with mean $\mu = 0$ and standard deviation $\sigma = 1$(May 2001). This equation is kept as simple as possible due to data limitations. The birth and death rates are separated, rather than using the net growth rate, because IGRs directly affect the birth rate, not the death rate. The birth rate of *Solenopsis* spp. is known to vary seasonally (Porter 1988), and we use a sine function to model this:

$$\boldsymbol{b}(\boldsymbol{t}) = \boldsymbol{B}\left(1 + \boldsymbol{M}\sin\left(2\pi\frac{\boldsymbol{t}-\boldsymbol{S}}{52}\right)\right), \tag{2}$$

where B is the average birth rate over 1 year, M is the magnitude of the variation in birth rate and S defines the time of year when the birth rate is greatest. The birth rate must be positive, i.e. $b(t) \geq 0$, and M is a magnitude, so must be non-negative. These conditions dictate that $B \geq 0$ and $0 \leq M \leq 1$.

The parameters $u_{IGR}, u_T, d_{dd}, B, M$ and S were fit to data (see Supplementary Information Table A.1) using Markov chain Monte Carlo (MCMC) in Python using least squares (full details in Supporting Information A). Due to the relatively small dataset available, we used other sources to set values for as many parameters as possible to minimise the chance of overfitting. While we are still fitting more parameters than preferred (given the data), there is no clear way to further simplify our model. We assume that IGR affects the population continuously for a fixed 4-week time interval, which is the application frequency in the eradication plan (Hodgson et al. 2014). The effect of the toxin does not last as long as the effect of the IGR, but its effect length is uncertain. Hence, we fitted our model with the toxin effect length of 1, 2 and 3 weeks separately. We use $d_n = 11.2$ as the natural death rate of ants (Asano and Cassill 2011). We do not vary d_n because the fitting procedure is essentially estimating the quantities $b(t) - d_n$ and $b(t)u_{IGR}(t)$; altering d_n would simply cause a change in the value of $b(t)$ and $u_{IGR}(t)$, without actually changing the model dynamics.

Detection model

The monitoring phase of the eradication, which aims to confirm the absence of ants, is implemented at the end of the baiting phase, both in the model and on-ground. The detection model estimates the probability that a lattice of lures will detect an ant colony. To calculate this, we first need to know the probability, p, that a lure will successfully detect a nearby colony. We believe that the likelihood of detecting a colony is primarily dependent on the ant abundance, $n(t)$. We use an exponential distribution to estimate the probability that a lure detected the presence of the tropical fire ant (McCarthy et al. 2013):

$$\boldsymbol{p} = 1 - \boldsymbol{e}^{-\boldsymbol{\alpha} \times \boldsymbol{n}(\boldsymbol{t})^{\boldsymbol{\beta}}}. \tag{3}$$

Model fitting was undertaken using maximum likelihood estimation. There were 80 sites and 6 trials at each site in the detection trial (see Supplementary Information Section B.1 for details), so, assuming that each trial is independent, a binomial likelihood function is the most natural choice. We use bootstrapping to estimate errors for α and β (Efron and Tibshirani 1994). This is done by generating 1000 samples of the 80 sites (with repetition), and finding the values of α and β that maximise Eq. (3). This results in 1000 estimates for each parameter, for which we report the standard deviation (see Supplementary Information Table B.3).

It has been established that ants are capable of finding a lure within a certain distance of the colony—the detection radius d_r—which is 3–4 m (Bellio 2007). For a lattice of lures to detect a single colony, at least one lure must detect presence of ants. Hence, the probability that ants are not detected (event $\bar{D}$), given that there are ants present (event A) is

$$\boldsymbol{P}(\bar{D}|\boldsymbol{A}) = \sum_{\boldsymbol{j}} \boldsymbol{P}(\boldsymbol{l} = \boldsymbol{j})(1 - \boldsymbol{p})^{\boldsymbol{j}}, \tag{4}$$

where $P(l = j)$ is the probability that there are j lures within the detection radius of the colony (as the position of the colony is unknown) and $(1 - p)^j$ is the probability that all j lures fail to detect the colony. We calculate $P(l = j)$ numerically for a given lattice of lures by considering all possible locations for a colony (see Supplementary Information Section B.2). The probability of detecting a colony increases as effort (number of lures) increases and the shape of this relationship is shown in Supplementary Information Figure B.5. This probability is conditional on the presence of ants. To get a probability of eradication, we use Bayes rule:

$$\begin{aligned}\boldsymbol{P}(\bar{\boldsymbol{A}}|\bar{D}) &= 1 - \boldsymbol{P}(\boldsymbol{A}|\bar{D}) \\ &= 1 - \frac{\boldsymbol{P}(\bar{D}|\boldsymbol{A})\boldsymbol{P}(\boldsymbol{A})}{\boldsymbol{P}(\bar{D}|\bar{\boldsymbol{A}})\boldsymbol{P}(\bar{\boldsymbol{A}}) + \boldsymbol{P}(\bar{D}|\boldsymbol{A})\boldsymbol{P}(\boldsymbol{A})}.\end{aligned} \tag{5}$$

The probability of not detecting ants given that there are no ants is set to 1 ($P(\bar{D}|\bar{\boldsymbol{A}}) = 1$), while $P(A)$ and $P(\bar{\boldsymbol{A}})$ are estimated from the population model, Eq. (1), and $P(\bar{D}|A)$ is estimated from Eq. (4).

Labour optimisation

Prior to any trips to Ashmore Reef Commonwealth Marine Reserve to check for the presence of ants, the number of staff deploying lures, or the number of detector dogs to purchase and train, must be decided. Having fewer staff reduces training and transport costs, but increases the time taken to complete the task, meaning high total overhead costs (e.g. cost of having a boat at Ashmore Reef). We estimate all the relevant costs (Supplementary Information Table B.4) and solve, in general, for the number of staff to hire and dogs to train (see Supplementary Information Section C):

$$\boldsymbol{L}^* = \sqrt{\frac{\text{overhead costs} \times \text{amount of work}}{\text{marginal travel cost} + \frac{\text{start} - \text{up cost}}{\text{numberofuses}}}}. \tag{6}$$

Here, L^* is the optimal amount of labour to use, which minimises the total costs. The overhead cost is the incurred cost per day when there are ongoing activities (e.g. the daily cost of having a boat at Ashmore Reef). The amount of work is the number of days that it would take one person to complete the task (e.g. the time it would take one person to deploy lures across all islands at Ashmore Reef). The marginal travel cost is the extra travel cost incurred when adding an extra person (e.g. the daily wage of one staff member, multiplied by the travel time). The start-up cost is the cost that must be paid to increase the number of staff (e.g. training costs). Finally, the number of uses is the number of times the activity will be repeated (e.g. number of trips to Ashmore Reef). In general, Eq. (6) will not return an integer and the total cost of the two closest whole numbers (either side of L^*) should be checked to see which is lowest.

Canine versus lure detection

There is no direct comparison of canine detection and lure detection for the tropical fire ant, so we estimate the costs of each method as a comparison. As the canine detection rate is uncertain, we repeat this analysis for canine detection probabilities ranging from 0.8 to 0.98 (Lin et al. 2011). The lure spacing is chosen, using Eq. (4), such that the detection probability matches the canine detection probability, and the number of staff is chosen using Eq. (6) to minimise the lure deployment cost. This is repeated for four values of canine detection probability and three values of the lure detection radius (3, 3.5 and 4 m).

Optimising monitoring effort

We take an economic approach to optimise the monitoring effort for achieving eradication (Regan et al. 2006; Rout et al. 2009a, b). This is done by minimising the total expected costs of the detection events and any subsequent work (see Supplementary Information Section D). The expected costs are the cost of the detection events themselves, along with any 'failure cost' associated with incorrectly declaring eradication:

$$\text{cost} = \text{detection cost} + \boldsymbol{P}(\boldsymbol{A}|\bar{D}) \times \text{failure cost}, \qquad (7)$$

where $P(A|\bar{D})$ is the probability that the eradication failed even though no tropical fire ants were detected. We use the projected cost of the eradication project as the failure cost, which is \$AUD 2.32 million (Hodgson et al. 2014). The value of $P(A|\bar{D})$ and the detection cost both depend on the amount of effort put into detection. We obtain the optimal detection effort by solving for the amount of detection effort which minimises the total cost, Eq. (7). We note that we solve for the optimal detection effort over two surveillance events when seeking to declare eradication, rather than looking at ongoing surveillance at the site (see Regan et al. 2006).

The optimal lure spacing to demonstrate eradication success, found by minimising Eq. (7), depends on the prior probability of eradication, the expected detectability of ants, the cost associated with failure and the detection radius, d_r. The upper limit on lure spacing is determined by ensuring any potential colony location would be within the detection radius of at least one lure (lure spacing $\leq \sqrt{3}d_r$ for a triangular lattice, or $\sqrt{2}d_r$ for a square lattice, see Supplementary Information Figure B.6). The optimal lure spacing also relies on the prior belief of eradication success. At the conclusion of the control phase it will be possible to use the population model to estimate this prior. However, the baiting regime is not finalised, so we model a range of prior beliefs, and we calculate the optimal lure spacing for three values of the detection radius.

Results

Population model and the probability of eradication success

Our population model showed a good fit to the pilot data (Fig. 3), parameter estimates are given in Table 1. The tropical fire ant abundance at Ashmore Reef varies seasonally, with ant abundance peaking towards the end of the wet season (April). We then simulate the probability of eradication using different baiting strategies (Fig. 4). For each scenario we draw 1000 parameter samples and run the stochastic population model 100 times. For each simulation we begin by simulating the population dynamics for 2 years to remove any effect of the initial condition. We then allow baiting to take place. This occurs monthly throughout the dry season months (we allow 5 possible baiting events) across 2 years—which accommodates a maximum of 10 applications (IGR and toxin can be applied simultaneously). As there are four islands at Ashmore Reef, and ants must be removed from all islands simultaneously, the plot is the probability of removal from a single island raised to the power of four. These simulations were run for 1000 parameter sets. This model shows that eradication is only likely if a combination of IGR and toxin is applied across the planned ten baiting events. Using IGRs exclusively has a 0% probability of success, while using only toxin has at best a 30% probability of eradication. Ten applications of IGR and five applications of toxin results in greater than 80% probability of eradication, and additional applications further increases this probability.

We conduct a sensitivity analysis to see how sensitive the estimated probability of eradication is to the parameters. We do this for three baiting strategies: 4, 5 and 6 applications of IGR and toxin. For each strategy we first run the model 100,000 times using the median parameter estimates. Then we adjust each parameter up and down, one at a time, to the 25th and 75th percentile value for that parameter from the posterior distributions. For each case (one parameter adjusted up or down and the remaining at their median values) we run the population model 100,000 times. The change in the probability of eradication for each parameter and number of baiting events is given in Fig. 5. Across all baiting regimes, the probability of eradication is most sensitive to the baiting

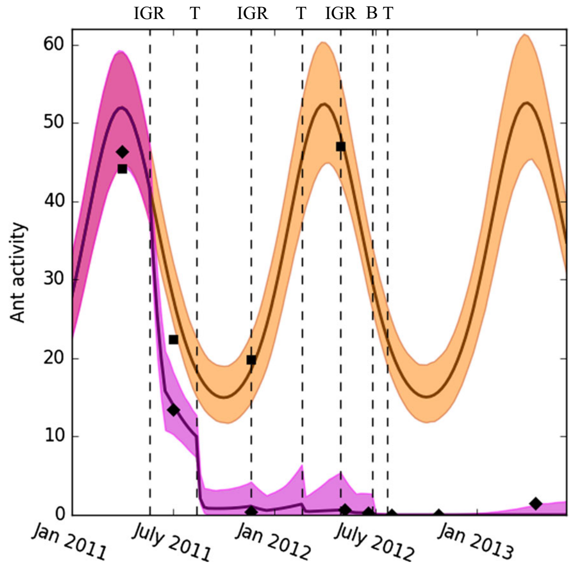

Fig. 3 Population model fit to the tropical fire ant abundance data during the pilot control period 2011–2012 on East Island (*orange*, *squares*) and Middle Island (*purple*, *diamonds*). The *solid lines* are the average of the stochastic model and *shaded areas* show the range of trajectories. The *solid dots* are ant abundance derived from each island-wide survey using a lattice of lures. For Middle Island only, the *dashed lines* are the baiting events. Baiting event 1, 3 and 5 involved *insect* growth regulator (IGR), baiting event 2, 4 and 7 involved toxins (T) and baiting event 6 involved a combination of IGR and toxin (B)

effectiveness parameters u_{IGR} and u_T. The next most important parameter is the average birth rate, R, particularly as the number of baiting events increases.

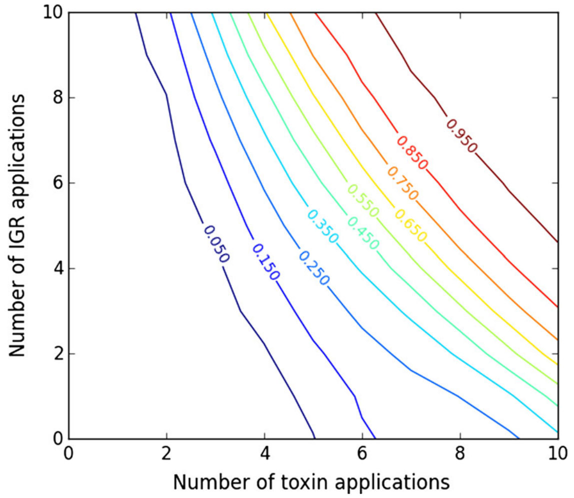

Fig. 4 The probability of tropical fire ant eradication across all islands at Ashmore Reef when the number of baiting events involving toxin and IGR are varied. *Colours* indicate different eradication probabilities

Relative cost of canine and lure detection

The total cost for lure and canine detection, over a range of parameters and number of detection events, is given in Fig. 6. (Although there are currently only two planned surveillance events, there may be other instances of detection events throughout the project.) The total cost increases linearly as the number of total detection events increases. We identified three detector dogs as the optimal team size (see Supplementary Information Section C.1). However, during any vessel-based visit to Ashmore Reef there is a work plan that imposes a minimum stay of 7 days (Hodgson et al. 2014). With this constraint, the optimal team size reduces to two detector dogs. The high start-up costs, but low ongoing costs, of canine detection mean that purchasing dogs is only justifiable if they will be used repeatedly (Fig. 6). With 10 detection events, canine detection is at least as cost effective as lure detection over the range of parameters considered.

Table 1 Population model parameter estimates for tropical fire ant dynamics, detection and eradication at Ashmore Reef (Eqs. (1) and (2)). The model fit was done separately for each value of toxin effect time. The model fit was done separately for each value of toxin effect time

	Toxin time = 1		Toxin time = 2		Toxin time = 3	
	Mean	95% credible interval	Mean	95% credible interval	Mean	95% credible interval
B	14.17	(14.01, 14.32)	18.29	(17.48, 18.98)	20	(19.05, 20.92)
M	0.2764	(0.2604, 0.2927)	0.3055	(0.2833, 0.3279)	0.3353	(0.3102, 0.3605)
d_{dd}	0.03488	(0.02982, 0.04059)	0.1650	(0.1405, 0.1871)	0.2170	(0.1863, 0.2471)
S	−25.15	(−25.36, −24.83)	−22.73	(−23.25, − 22.20)	−22.35	(−22.94, −21.73)
u_{IGR}	0.7203	(0.6298, 0.8125)	0.6063	(0.5291, 0.6855)	0.5336	(0.4516, 0.6157)
u_T	38.83	(36.69, 39.93)	39.34	(38.02, 39.96)	38.70	(36.43, 39.92)

Optimising detection through the spacing of lures

The higher the failure cost, the more effort needs to go into ant detection, thus decreasing the lure spacing. Each other quantity works to increase lure spacing. A large detection radius or high ant detectability makes detection easier, meaning less effort needs to go into detection. Finally, the higher the prior probability of eradication the less effort should go into detection (Fig. 7). We find that the larger the prior probability of eradication, the lower the required surveillance effort. The optimal lure spacing is different for the two surveillance events because if ants are present, their abundance, and thus their detectability, will increase through time.

Discussion

Our framework uses two distinct but dependent models, a population model and a detection model, to help inform decisions for an eradication project. In this paper we have applied it to the proposed eradication of tropical fire ants from Ashmore Reef Commonwealth Marine Reserve, increasing the understanding of how different baiting schedules affect the probability of eradication; demonstrating that purchasing and training two detector dogs would result in lower detection costs, if they are used sufficiently often; and developing a method to optimise the spacing of lures when confirming eradication. As this work was completed at a very preliminary stage of the project, we have less data than is ideal, particularly for the population model, and we simplified the model as much as possible to avoid overfitting. However, the sensitivity analysis does indicate that more must be completed to better understand the relative effects of IGR and toxin. Despite these limitations, our data are typical of that available to managers overseeing eradication programs prior to commencement. It is envisaged that as the program progresses, more data will become available which can be used to test and refine the models. For example, following any baiting, follow up surveys will take place to monitor the decline in ant abundance. This would then feed into our population model to improve estimates of population dynamics, along with bait efficacy. In that sense, our results provide project management guidance, but should not be considered a final product—rather the product is the model itself. Importantly, this analysis sets a foundation for future work on the islands and will allow the models to be updated and improved in an adaptive management framework (Allen et al. 2011).

Detection and monitoring for invasive species management has received considerable research attention. Much of this focuses on optimising surveillance effort to detect new invaders before they become established (Brown et al. 2004; Barrett et al. 2009; Davidovitch et al. 2009; Jarrad et al. 2010, 2011; Stringer et al. 2011; Whittle et al. 2013) and how to balance these monitoring costs with quarantine and control costs (Moore et al. 2010; Rout et al. 2011, 2014b). This differs from the monitoring

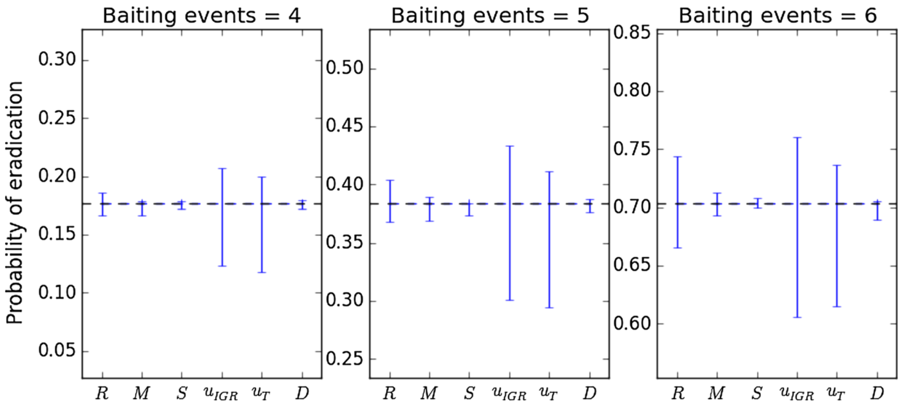

Fig. 5 Sensitivity analysis for the population model. The *horizontal dashed line* shows the probability of eradication with all parameters at their median values. The *vertical bars* show the variation to the probability of eradication caused by altering that parameter to the 25th or 75th percentile

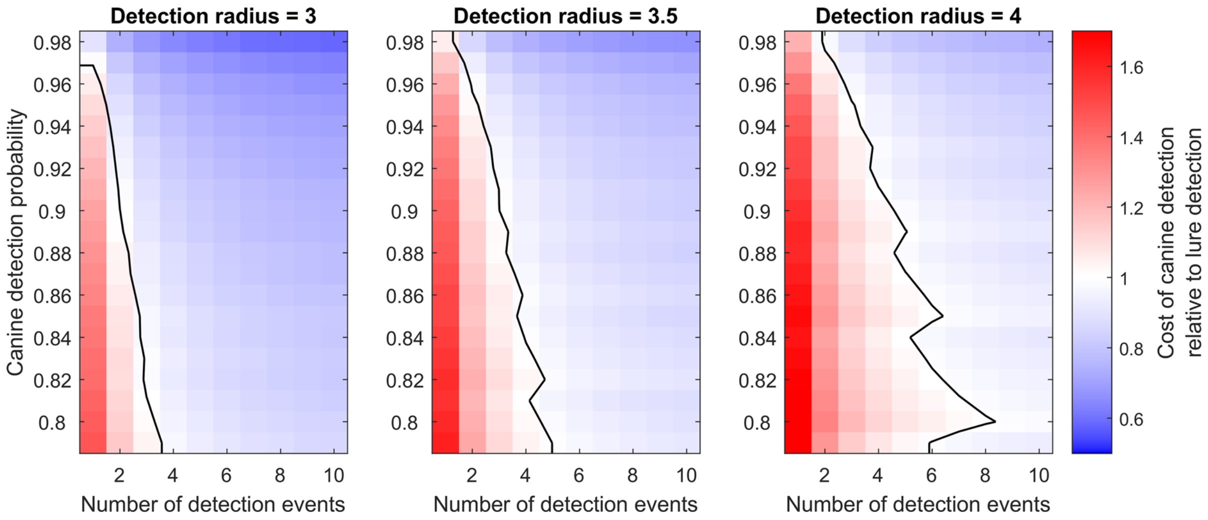

Fig. 6 Comparison of the costs of lure detection and canine detection. Results are presented at a range of detection radii (d_r) and dog detection probabilities with the cost-effectiveness of each method dependent on the number of detection events. The *shaded blue regions* (*top right of each plot*) show where canine detection is cheaper, and the *red, region* (*lower left of each plot*) shows when lure detection is cheaper. The *solid black line* dividing these areas depicts when the costs of the two methods are equal. These results are for low ant abundance ($n = 1$); see Supplementary Information Section C.3 for results with higher abundances

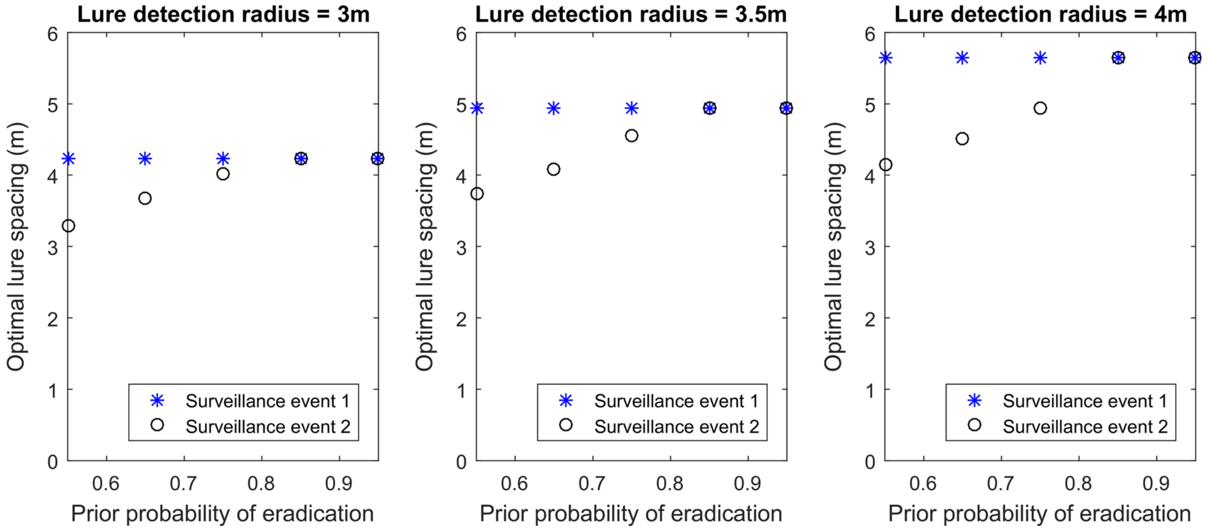

Fig. 7 The optimal lure spacing to determine eradication success, with the constraint that all locations on each island at Ashmore Reef must be within the detection radius of a lure. *Each plot* is for a different detection radius, and the *blue stars* and *black circles* show the optimal lure spacing for the first and second surveillance event respectively. In these plots the ant abundance is 1 for surveillance event 1 and 21.2 for surveillance event 2, in *line* with the population model

problem in this paper, where we seek to set monitoring effort to confirm eradication (see Ramsey et al. 2009, 2011; Rout et al. 2014a). Our model of ant detection assumes that lures are placed in a regular arrangement. Even though irregular placement can be effective, when deploying in high-densities, regular placement is more effective (Berec et al. 2014). There are improvements that could be made to ant detection in the future, including leaving lures out for longer (Ward and Stanley 2013), using unmanned aerial vehicles (Lei et al. 2015) and canine detection (Brooks et al. 2003; Lin et al. 2011). In this paper we found conditions under which canine detection may outperform lure detection, but other strategies and methods may also warrant consideration. We also note that the value of canine detection probability that we used, 0.9, is conservative, and dogs may prove economically superior with fewer detection events. We also expect low ant abundance once control commences, which hinders lure detection in the model. However, provided that there are enough detection events, then detector dogs are more cost-effective over time frames typical of such projects. Although we do not focus on post-eradication monitoring for the reinvasion of tropical fire ants, or other species, it is an important aspect of island management that will need to be addressed upon successful removal of tropical fire ants and could be included in this modelling framework at a later stage.

Invasive species eradications often deliver important positive conservation outcomes (Jones et al. 2016; McCreless et al. 2016; Doherty et al. 2016). Ant eradications are becoming more frequent with time and eradication of infestations on larger islands are becoming successful (Hoffmann et al. 2016). These projects are expensive, with project costs regularly in the millions of dollars (Holmes et al. 2015). Our framework is applicable for many other island eradications where it could be used to help reduce costs and improve outcomes. Our models are also applicable elsewhere, for example our detection model can be applied in other situations where lures are used, and our method to calculate the optimal number of dogs and staff (see Supplementary Information Sections C.1 and C.2) can be applied elsewhere to find the optimal investment in labour. Ideally the framework could be used to optimise invasive species control decisions and surveillance investment from the outset. This requires costs and values to be ascribed to every aspect of the project, which is not always straightforward. In the context of Ashmore Reef, this would include placing a value on the impacts of toxin on non-target species. Currently, these impacts are not fully understood and deciding the acceptable damage to native flora and fauna in the process of eradication is complex and controversial (Lampert et al. 2014). Some of this falls under political decisions; while our models can predict the outcome of various baiting regimes, it is up to management to decide what non-target impacts are acceptable. The best way to proceed is to develop potential scenarios at collaborative workshops with scientists and managers, which would then be analysed carefully. Nevertheless, developing interacting models for population control and detection with pilot data can provide material benefits to eradication programs. Contributions include outputs that provide clear justification for decisions and the laying of a foundation for adaptive management, and identification of future priorities with respect to ongoing data collection and modelling.

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