

Using the Spatial Population Abundance Dynamics Engine for conservation management

Nicholas J. Beeton^{1*}, Clive R. McMahon^{2,3}, Grant J. Williamson¹, Joanne Potts⁴, Jonathan Bloomer⁵, Marthán N. Bester⁶, Larry K. Forbes⁷ and Chris N. Johnson¹

¹School of Biological Sciences, University of Tasmania, Hobart, TAS 7001, Australia; ²Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman, NSW 2088, Australia; ³Institute of Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7001, Australia; ⁴The Analytical Edge Pty Ltd., PO Box 47, Blackmans Bay, TAS 7052, Australia; ⁵Department of Nature Management, Centurion Academy, Charles de Gaulle Street, Centurion 0048, South Africa; ⁶Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Hatfield 0028, South Africa; and ⁷School of Mathematics and Physics, University of Tasmania, Hobart, TAS 7001, Australia

Summary

1. An explicit spatial understanding of population dynamics is often critical for effective management of wild populations. Sophisticated approaches are available to simulate these dynamics, but are largely either spatially homogeneous or agent based, and thus best suited to small spatial or temporal scales. These approaches also often ignore financial decisions crucial to choosing management approaches on the basis of cost-effectiveness.
2. We created a user-friendly and flexible modelling framework for simulating these population issues at large spatial scales – the Spatial Population Abundance Dynamics Engine (SPADE). SPADE is based on the Spatio-Temporal Animal Reduction (STAR) model (McMahon *et al.* 2010) and uses a reaction–diffusion approach to model population trajectories and a cost-benefit analysis technique to calculate optimal management strategies over long periods and across broad spatial scales. It expands on STAR by incorporating species interactions and multiple concurrent management strategies, and by allowing full user control of functional forms and parameters.
3. We used SPADE to simulate the eradication of feral domestic cats *Felis catus* on sub-Antarctic Marion Island (Bester *et al.*, South African Journal of Wildlife Research, 32, 2002, 65) and compared modelled outputs to observed data. The parameters of the best-fitting model reflected the conditions of the management programme, and the model successfully simulated the observed movement of the cat population to the southern and eastern portion of the island under hunting pressure. We further demonstrated that none of the management strategies would likely have been successful within a reasonable time frame if performed in isolation.
4. Spatial Population Abundance Dynamics Engine is applicable to a wide range of population management problems and allows easy generation, modification and analysis of management scenarios. It is a useful tool for the planning, evaluation and optimisation of the management of wild populations and can be used without specialised training.

Key-words: demography, eradication, *Felis catus*, invasive species, scenario building, spatial ecology, wildlife disease

Introduction

Conservation management deals with a broad, complex and rapidly evolving range of threats to environmental values including climate change, habitat loss, wildlife disease and invasive species. Management decisions are often by necessity based on limited field research, relying instead on expert opinion or even anecdotal data, and are implemented within social, political and cultural contexts that can limit their scale and range. A major challenge for the research community is therefore to provide robust predictions on how populations will respond to various management interventions from this

limited information. The consequences of population mismanagement often spread far beyond the dynamics of the species in question, into the surrounding ecosystem and beyond. It is therefore important that management recommendations are transparent, objective, based on the best-available information, and flexible enough that plans can be changed when new information comes to light.

Several modelling approaches have been developed to assess population responses to management and to compare prospective management strategies (e.g. McMahon *et al.* 2010). These models have been used for a wide array of conservation issues such as the spread and control of wildlife disease (Beeton & McCallum 2011) and livestock diseases where wildlife may act as a reservoir host (Bradshaw *et al.* 2012), control of invasive species (McMahon *et al.* 2010) and wider ecosystem effects

*Correspondence author. E-mail: nicholas.beeton@utas.edu.au

due to interactions between species (Courchamp, Langlais & Sugihara 1999; Pellissier *et al.* 2013).

Models available for simulating population management are often either not used or not effectively incorporated into management planning. Despite some notable exceptions such as VORTEX (Lacy & Pollak 2014), Maxent (Phillips, Anderson & Schapire 2006) and NetLogo (Wilensky 1999), most approaches require substantial expertise to build, run and interpret the models. Those that are user friendly are often used carelessly, leading to results that are either misleading, incorrect or highly uncertain (discussed in Harris *et al.* 2013; Gould *et al.* 2014). As a result, most successful publications in the field have made general recommendations (Fletcher & Westcott 2013), avoiding specific predictions or management suggestions that may not be justifiable.

Incorporating and accounting for spatial heterogeneity is becoming increasingly valuable in population models, especially in wildlife disease and invasive species management. There is a broad literature on spatially explicit dynamic models (e.g. rabies in raccoons: Smith *et al.* 2002; Russell *et al.* 2005), but these models are largely either individual-based or probabilistic in nature. While these methods are flexible and powerful, they generally require detailed data, which is often lacking. These approaches are also computationally intensive, making detailed scenario building and sensitivity analyses difficult.

Reaction–diffusion population models (Fisher 1937) provide a deterministic model framework capable of simulating a variety of biological phenomena (Volpert & Petrovskii 2009). In particular, they can be used to model population and disease dynamics simultaneously (Murray, Stanley & Brown 1986; Murray 1989). The spatial diffusion in these models is equivalent to a random walk, or a Gaussian dispersion kernel. Reaction–diffusion models have been well defined and numerically tested (e.g. Bendahmane & Langlais 2010), particularly for disease spread (e.g. Wang & Zhao 2011), and have been shown in some simplified cases to agree with field observations (Dwyer 1992). In the two-dimensional case, however, reaction–diffusion models are seldom used in applied population biology – this is probably due to some combination of a lack of spatially specific data to populate and validate such models, the current dominance of individual-based and probabilistic models and the mathematical complexity involved in developing such models. An exception is the Spatio-Temporal Animal Reduction (STAR) model (McMahon *et al.* 2010), developed for planning of management of invasive animals in Kakadu National Park, but intended to be adaptable for use in other cases (Wiggins *et al.* 2014). STAR is essentially a discrete-time analogue of a reaction–diffusion system and is to our knowledge the first such model simulating the effects of different management options in a real-life case study.

We introduce the Spatial Population Abundance Dynamics Engine (SPADE), a tool for both modellers and managers to explore the outcomes of population processes and management interventions. Like STAR, SPADE was designed as a user-friendly tool to model invasive species and their management. Our model is written using the R programming language (R Core Team 2014; packages referenced in Appendix S2,

Supporting Information) and features a graphical user interface (GUI). Using it requires only some basic knowledge of the species' biology and basic familiarity with Geographic Information Systems (GIS; See Appendix S1 for manual). However, the modelling framework is sufficiently flexible that it can model infectious disease as well as interspecific interactions such as competition and predation or intraspecific interactions between distinct cohorts of the same species. Detailed, unbiased field data at the scale needed to validate demographic models are uncommon (e.g. wildlife disease: McCallum, Barlow & Hone 2001). Inexact but qualitatively reasonable estimates of population dynamics are much more easily obtained. For these reasons, SPADE is not designed to calculate accurate population abundance measures based on exact measurements, but instead to estimate and compare larger-scale patterns based on best-available estimates and assumptions.

Feral domestic cats *Felis catus* (Linnaeus 1758) are among the most devastating invasive pests and are wholly or partly responsible for the decline or extinction of numerous species, particularly in Australia (Lowe *et al.* 2000). Their impacts on native fauna are amplified on islands: cats have been identified as the primary driver of extinction for at least 33 island endemics world-wide (Nogales *et al.* 2013).

The eradication of feral cats on Marion Island (290 km²), a South African sub-Antarctic territory (Fig. 1), is the largest island eradication of cats to date (Nogales *et al.* 2004). A multi-phase eradication programme was planned in 1974–1976 and implemented over more than 15 years, commencing with biological control using the feline panleucopaenia virus (1976–1977) and concluding with intensive hunting (1986–1989), trapping and poisoning (1989–1993) (Bester *et al.* 2002).

We selected this as our case study for a number of reasons. The final stages of the programme were meticulously documented: sighting, shooting and trapping events were recorded for each hunting trip with the date and grid coordinates of occurrence (to half-arcminute resolution, with each grid cell approximately 600 × 900 m). The island is sufficiently large that, based on studies of home ranges which suggest a range of at most 0.3 km² (Barratt 1997), individual cats are unlikely to travel regularly across the entire island; cat movement around the island is more likely to occur over the course of several generations. This makes the process amenable to deterministic techniques, as individual heterogeneity in dispersal patterns can be expected to 'wash out' on a larger temporal or spatial scale. Although only 3 years of data exist for which there are reasonable numbers of cats in the landscape, this is likely to be sufficient time for some measurable effects of dispersal to be seen.

Materials and methods

We estimated the density of cats in each cell across the island at the start of the hunting phase in 1986. We then used SPADE to fit a spatially explicit population model to the sighting and culling data during the hunting phase. We tested whether the model captured both the local and island-wide population dynamics in this period, looked for evidence of population suppression as a result of feline panleucopaenia

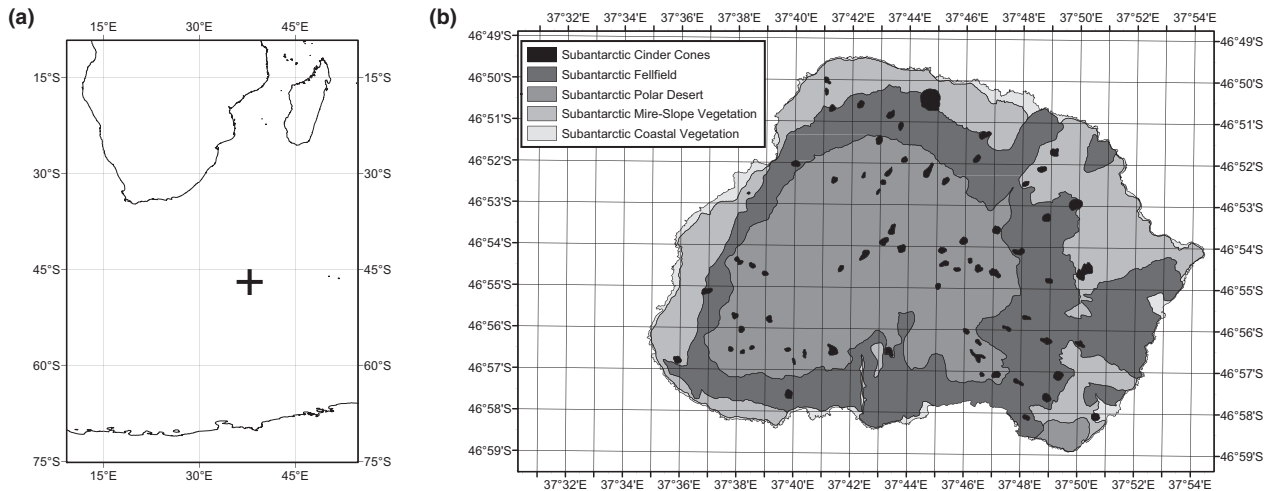


Fig. 1. Location of Marion Island between South Africa and Antarctica (a) and a map of the island describing its five main vegetation types (b).

based on the best-fitting model parameters and examined some additional management scenarios.

MODEL DESCRIPTION

Finding the population density (defined here as X) of a species in time (t) and space (x and y in two-dimensional space) based on its demographic and dispersal information can be represented as a Cauchy problem. That is, $X(x, y, t)$ requires an initial condition $I(x, y)$ to be specified across our spatial domain of interest (C) at a specified time (t_0), such that

$$X(x, y, t_0) = I(x, y) \text{ for all } (x, y) \text{ in } C, \quad \text{eqn 1}$$

and a partial differential equation (PDE) that will determine future values of the population at each point in C for $t > t_0$. We also assume that the population has a nonzero carrying capacity, or equilibrium, $K(x, y)$ such that the population density remains stationary everywhere if set to this equilibrium – or

$$\frac{\partial X(x, y, t)}{\partial t} = 0 \text{ where } X(x, y) = K(x, y) \text{ for all } (x, y) \text{ in } C \text{ and } t > t_0. \quad \text{eqn 2}$$

Our model uses the method of lines approach to integrate the necessary PDE to calculate population trajectories. It separates the population into smaller but finitely many connected subpopulations, for which the local dynamics are calculated at each time step. The diffusion component is simultaneously calculated using a second-order finite difference of the Laplacian, namely

$$\nabla^2 Z_{i,j}(t) = \frac{Z_{i+1,j}(t) + Z_{i-1,j}(t) - 2Z_{i,j}(t)}{(\Delta x^2)} + \frac{Z_{i,j+1}(t) + Z_{i,j-1}(t) - 2Z_{i,j}(t)}{(\Delta y^2)}, \quad \text{eqn 3}$$

where $Z_{i,j}(t)$ represents some function of the number of animals in the population at cell location (i, j) and time t , and Δx and Δy are the width and height of each cell. This diffusion approach for modelling dispersal is similar to that used in STAR. Some formulae commonly used in modelling local population dynamics and dispersal have been included in the GUI, and for advanced users, SPADE is also capable of using any formulae describable in R syntax. In the case study presented here, we used a density-dependent logistic model

as a parsimonious estimate of demographic dynamics. We then used a discrete-space analogue of the reaction–diffusion model described in Korobenko, Kamrujjaman & Braverman (2013) which, like the demographic part of the equation, also has a fixed point at a carrying capacity $X = K$ in order to satisfy eqn 2:

$$\frac{\partial X}{\partial t} = (b - \mu)X \left(1 - \frac{X}{K}\right) - rX + D\nabla^2 \left(\frac{X}{K}\right), \quad \text{eqn 4}$$

where we have used X as population density as with eqns 1–2. The fecundity b and removal rate r are kept as free variables as the effect of the virus and culling, respectively, are not entirely known at the relevant stage of the programme, whereas the mortality μ is assumed to be 1, representing a mean cat life span of 1 year (Warner 1985; see Appendix S3 for details). As we are modelling discrete cells spatially (eqn 3), the diffusion coefficient D has units of cats per year in our particular case, which can be interpreted as a rate of spread in area per year multiplied by the local carrying capacity in cats per unit area (Korobenko, Kamrujjaman & Braverman 2013). Our model is capable of modelling in continuous time, thus modelling all processes simultaneously, via this approach, whereas STAR models demographic and dispersal processes sequentially every season.

Removals are modelled by SPADE in three different ways: proportional, absolute and capped proportional. Our case is modelled with proportional management, which removes a fixed proportion of the population from each cell continuously, while ensuring the population density in each given cell does not fall below a user-specified target density (details in Appendix S2). These management strategies are controlled by a user-defined gridded mask that specifies which cells are to be managed and to what extent, in comparison with other managed cells. During the simulation process, the model keeps track of the total number of animals ($c_{t,x}$) culled over the course of a timestep in each cell for later use along with the numbers remaining ($N_{t,x}$). Similarly, given relevant information to parameterise a cost-per-animal relationship for removal at differing animal densities (e.g. Pople *et al.* 1998), the model is able to measure the cost of management and use this information to assist in various optimisation routines based on those used in STAR.

CASE STUDY

As mentioned, SPADE requires an estimate of initial conditions in order to be able to predict cat abundance over time. We set the t_0 for

this initial condition to be August 1986, immediately before the beginning of the full-scale eradication plan. This is the point at which explicit monitoring data were first available and at which the cat population had stabilised after the introduction of the feline panleucopaenia virus (Bester *et al.* 2002).

Sighting data are likely to be biased, depending on visibility of animals in different habitat types. While data from trapping also have biases – in particular, differences in trappability between individuals – traps are more likely to be equally visible and attractive to cats in different habitats, so we assumed that trapping success indicates abundance. To address the potential sighting bias, we created models for both the trapping and sighting process incorporating habitat and simple exponential decrease in population over time for both sources, as well as

The model for trapping is necessarily more complex than that for sighting for several reasons. As with the sighting model, the capture frequency may also depend on the habitat type for cats ($\lambda_{c,v}$) and other animals ($\lambda_{o,v}$) and the mean date of the trapping survey for a given observation \bar{t} via the decline rate λ_t . However, no explicit habitat information was given for each trap, so the model based the probability of a trap being in a particular habitat type $p(v)$ on the relative amount of each habitat in its cell. In addition, the trapping frequency may also be dependent on the lure l and/or bait b used in the trap via modifiers λ_l and λ_b . Finally, most traps are set off and reset more than once across the monitoring period.

A likelihood function was created using a statistical model based on all of the above and is expressed in the most complex case as:

$$L(\{\lambda_{c,v}, \lambda_{o,v}, \lambda_t, \lambda_l, \lambda_b\} | \{r, p(v), t, \bar{t}, l, b\}) = \prod_{\text{observations}} \sum_v p(v) \begin{cases} \exp(-(\lambda_{c,v} + \lambda_{o,v})\lambda_l\lambda_b t e^{-\lambda_t \bar{t}}) & \text{if trap not sprung} \\ \frac{\lambda_{c,v}}{\lambda_{c,v} + \lambda_{o,v}} (1 - \exp(-(\lambda_{c,v} + \lambda_{o,v})\lambda_l\lambda_b t e^{-\lambda_t \bar{t}})) & \text{if cat} \\ \frac{\lambda_{o,v}}{\lambda_{c,v} + \lambda_{o,v}} (1 - \exp(-(\lambda_{c,v} + \lambda_{o,v})\lambda_l\lambda_b t e^{-\lambda_t \bar{t}})) & \text{if other} \end{cases} \quad \text{eqn 6}$$

potential effects of different lures and baits for the trapping data. Here, the island's five vegetation classes were used to define habitat types (Coastal Vegetation, Mire-Slope Vegetation, Fellfield, Cinder Cones and Polar Desert; Smith & Mucina 2006) in combination with two classes of altitude (above and below 100 m). Excluding Coastal Vegetation above 100 m by definition, this resulted in $5 \times 2 - 1 = 9$ unique habitat classes.

As trapping did not begin until later in the programme, we were required to compare the parameters of the trap model and sight model for the time period over which both methods were used (from January 1989 to April 1990). We then estimated the level of sighting bias by habitat as compared to the trapping data and used this bias factor to back correct the remaining sighting data to create an index of abundance for cats in 1986, which could then be used as an estimated initial condition for the model.

STATISTICAL MODEL OF CAT SIGHTING

Sighting of cats was assumed to be a Poisson process, with detection frequency λ at a particular cell c calculated by

$$\ln(\lambda) = \ln(t_c) + \ln(\lambda_v) - \lambda_t \bar{t}_c \quad \text{eqn 5}$$

in the most complex case. Here t_c is the number of minutes of detection effort expended in the target cell, λ_v the detection frequency per minute in habitat type v , λ_t the rate of decrease in detection frequency assuming an exponential decrease in population over time, and \bar{t}_c the mean of the number of days since hunting began taken across the sighting attempts in the cell. Simpler versions were run excluding the time-dependent term $\lambda_t \bar{t}_c$ and/or habitat dependence in the term $\ln(\lambda_v)$. A Poisson generalised linear model was fit to the data for each model, and Akaike information criterion (AIC) values were taken using the likelihood function and the best-fit parameters.

STATISTICAL MODEL OF CAT TRAPPING

Trapping can also be analysed as a Poisson process; that is, a continuous time process in which some event can occur at any time. However, only one cat – or other animal – can set off the trap, after which no further capture events are possible until the trap is reset.

and maximum-likelihood parameters were then found for the model in eqn 6 along with simpler models incorporating combinations of time, habitat, lure and bait.

SIGHTING BIAS CORRECTION

The best-fitting sighting and trapping models were then selected using the AIC. For the best-fitting models, standard errors for each habitat type were estimated using the Fisher information at the maximum-likelihood estimates in order to ascertain significance of results. The best-fitting trap-sight ratio (TSR), defining the number of trapping events likely to occur per sighting event over the same time period, was then calculated for each habitat type. These ratios were multiplied with the sighting rate for cats in 1986 to obtain an estimate of the expected trapping rate in each cell, which we treated as a proportional measure of abundance. Our initial estimate of the total population of cats on the island was taken from the estimate in Bloomer & Bester (1992) of 615 cats in 1982, but we treated this as a free parameter as the available data do not agree well with this estimate.

MODEL FITTING

Once a suitable initial condition was generated as described above, we were able to run simulations of the hunting programme in SPADE using a small number of free scalar parameters. The model was run with outputs every month and hunting simulated only in months where at least some hunting took place based on field data. We then used two separate data sets and statistical models to estimate goodness-of-fit and find best-fit model parameters.

Kill records

The first data set is the record of successful kills by the hunting programme. This was compared with a SPADE model assuming a constant monthly rate of removal in each cell (as per eqn 4), scaled by the recorded number of kills in each cell over the duration of the hunting programme. This model assumed that hunting in each cell is performed at a constant rate across time but a varying rate spatially due to accessibility. This spatially explicit hunting rate was taken from the total

number of culls in each cell across the entire hunting programme and scaled by a free parameter (the ‘relative culling rate’). A likelihood function suitable for use as a goodness-of-fit function was calculated using the probability of observing the real number of culls at each cell at each timestep given the simulated number of culls returned by the SPADE model at that timestep, specifically:

$$\ln(L(\theta|k)) = \sum_{t,x} \ln(\text{Pois}(k_{t,x}; \lambda = c_{t,x}(\theta))), \quad \text{eqn 7}$$

where $k_{t,x}$ represents the number of observed culls at timestep t and cell x ; $c_{t,x}$ represents the simulated cull at the same timestep and cell; and θ represents the remaining free model parameters in SPADE described in eqns 1–4 – namely the rate of dispersal D (eqn 4) in the cat population, the total initial population size (i.e. the sum of $I(x,y)$ in eqn 1), the maximum monthly culling rate (based on r in eqn 4) and the population growth rate ($b-\mu$ in eqn 4). This measure of fit is particularly useful in determining absolute patterns of population change, as the culling data provide exact information about what is happening in the population over time.

Observation records

The second data set is the record of each individual hunting trip i on date t_i over a number of identified cell locations x . These data comprise the number of cats observed (not necessarily shot at or killed) $n_{i,x}$ in each cell during the hunting trip, and the number of minutes of search effort $e_{i,x}$. These data were compared with SPADE’s estimate of population size $N_{t_i,x}$ for the month in which the hunting trip was performed, using the same modelling framework as described above. The likelihood function here was calculated from the probability of observing the real number of cats for each hunting trip given a constant probability of detection defined by the predicted number of cats in the cell and the amount of time spent in the cell.

$$\ln(L(\theta|\{n_{i,x}, t_i, e_{i,x}\})) = \sum_{i,x} \ln(\text{Pois}(n_{i,x}; \lambda = \lambda_{\text{scale}} N_{t_i,x}(t_i; \theta) e_{i,x}(\theta))). \quad \text{eqn 8}$$

Here θ again represents the free model parameters in SPADE, but this time excepting the total initial population size. This is because we introduced λ_{scale} as a constant scaling parameter designed to maximise the overall likelihood given the other data, defined as

$$\lambda_{\text{scale}} = \frac{\sum_{i,x} n_{i,x}}{\sum_{i,x} N_{t_i,x}(t_i; \theta) e_{i,x}}. \quad \text{eqn 9}$$

We introduced this because we cannot separate the effects of population size from overall detectability in the statistical model. Instead, we used the scaling parameter to ensure that the results are as realistic as possible, meaning that this measure of fit is solely useful to determine relative patterns of population change in contrast to the other data set (see Appendix S3 for details).

Both of these likelihood functions are simple representations of a complex process and as such are not perfect depictions of reality. Not only does the model contain assumptions and approximations that cannot be entirely the case (as with any other mathematical model of reality), it is also a deterministic model simulating a stochastic process, so cannot capture all of the complexity inherent in the data sets and landscape. The functions are instead intended as approximations used to find plausible model parameters.

Results

STATISTICAL MODELS

The results in Table 1 demonstrate that Habitat + time and Habitat + time + lure + bait are the most suitable sighting and trapping models, respectively, by AIC. Models including habitat were most suitable in all cases, suggesting habitat as the main driver of differences in frequency of sighting and trapping. For both best-fitting models, multiple pairwise differences between habitat types were found with P -values well below 0.05 after Bonferroni correction.

Sighting and/or trapping rates were unavailable due to lack of observations for four of the nine previously described habitat types, representing 6% of the island’s area. The estimated TSR for the remaining five types is given in Table 2. A high value for the ratio means that trapping was more successful than sighting and vice versa. As might be expected, for example, cats were more easily sighted than trapped in sparsely vegetated Mire-Slope Vegetation areas and the converse occurred in more densely vegetated Coastal Vegetation. As such, the sightings in Mire-Slope Vegetation areas in particular are weighted downwards by correction. For the four habitat types where there was insufficient data for the TSR to be calculated, cats were assumed to be absent and the ratio set to zero. As a result, any sightings that did occur in these areas in the initial year were given zero weight in the corrected abundance index.

SPADE MODELLING

Two independent goodness-of-fit methods were used to find parameters for the SPADE model that best fit the available data. The results were similar for both methods (Table 3), predicting a population with zero natural growth rate and diffusion at a rate equivalent to each cat moving up to approximately 2 km per year, the maximum rate possible for the current model formulation without losing numerical stabil-

Table 1. Goodness-of-fit for four models compared to sighting data and eight different models compared to trapping data, with model weights based on Akaike information criterion (AIC) scores

	Number of parameters	AIC	Model weighting
Sighting model ($n = 425$ cells, cats sighted = 321)			
Habitat + time	10	1537.0	1
Habitat	9	1576.4	<0.0001
Time	2	1655.4	<0.0001
Constant rate	1	1701.5	<0.0001
Trapping model ($n = 2386$ trap checks, cats trapped = 269)			
Habitat + time + lure + bait	17	2858.7	1
Habitat + time	11	2866.9	0.017
Habitat + lure + bait	16	2871.5	0.0016
Habitat	10	2882.5	<0.0001
Time + lure + bait	9	2983.0	<0.0001
Time	3	2989.4	<0.0001
Lure + bait	8	2996.6	<0.0001
Constant rate (cat + others)	2	3012.7	<0.0001

Table 2. Values for trap-sight ratios with confidence intervals for the five habitat types where data exists, defined by a combination of vegetation type and altitude

Vegetation type	Altitude	Trap-sight ratio (95% confidence intervals)
Mire-slope vegetation	High	0.0020 (0.0011–0.0039)
Mire-slope vegetation	Low	0.0024 (0.0013–0.0045)
Fellfield	High	0.0057 (0.0033–0.0096)
Fellfield	Low	0.0068 (0.0027–0.0168)
Coastal vegetation	Low	0.0176 (0.0075–0.0413)

Table 3. Best-fit parameters and maximum log-likelihoods for both goodness-of-fit methods. Note that the sighting per effort model relies on a relative measure of abundance so does not include a parameter for total carrying capacity

	Diffusion (cats/year)	Carrying capacity	Relative cull rate	Annual growth rate	Maximum log-likelihood
Sighting per effort	5.00	N/A	0.234	0.000	–7308.4
Culling	5.00	1508	0.355	0.000	–3054.7

ity (see Appendix S3). Although the best-fit cull rate differed between the methods, examination of profile likelihoods (Fig. 2c) suggests that a rate between the two maxima could provide a reasonable fit. We chose 0.3 as a compromise, it being within three points of the maximum likelihoods for both methods. Only one of the methods provided a measure of carrying capacity, which was predicted to be about double that estimated in the literature (615 ± 107 ; cited in Bloomer and Bester 1992).

Maximum-likelihood approaches discover the parameters that give the best fit to data given a particular model, but provide no evidence that the modelling framework itself is a reasonable representation of reality. In Figs 3–5, we used some summaries of the data and model fits to examine the overall goodness-of-fit visually.

Using SPADE's predictions of density in each cell, we then estimated the predicted number of captures in each cell for each field trip based on the length of time spent in that cell and compared this with the actual number of captures recorded in Fig. 3a. By comparing these results with 100 simulations of data that might be expected based on the SPADE densities, it is clear that even the best-fitting model overpredicts the number of captures at high densities. This may be due to incorrect assumptions in the model process but may also be caused by inaccuracies in the estimated initial condition (Fig. 5a), which is noisy due to lack of data in some places on the island.

We also tested the model fit by plotting a summary of the number of cats killed in each month of hunting. The model assumed that culling was undertaken on a set proportion of the population in each cell at any given time. This simplistic assumption appears to perform surprisingly well, with the observed data largely within the range of outputs expected from the model (Fig. 3b) except at the start, where the number

of culled cats fluctuates wildly from month to month. This discrepancy is not necessarily caused by the model process itself and may be due to additional unmodelled random effects such as spatial variation in locations of hunters, familiarity with the habitat and island; and other external factors such as weather, time of year and accessibility.

We then found best-fit models in the case where the diffusion parameter was set to zero for comparison. In both cases, the maximum log-likelihoods were at around 40 points lower than for the unrestricted cases (Table 4), suggesting a far less parsimonious fit. In addition, the summary plot for culling rates (Fig. 4b) demonstrates that without diffusion the best-fit model tended to under-predict the reduction in cat numbers over the course of the programme.

The spatial progression of the population based on sightings is shown and compared with the modelled results in Fig. 5. Here, the compromise model was used (with cull rate set to 0.3) and the model runs for longer than previously in order to compare with later surveys. As expected, the model appears to over-predict the overall population size particularly in the final two columns (see Fig. 5k,l) as by this stage trapping and poisoning had also been introduced, which was not represented in the model. It is difficult to pick out general spatial trends as the sighting data are quite noisy and vary substantially spatially from season to season. Despite this, the model successfully predicted an eventual contraction to the southeast of the island (see Fig. 5f,l).

When hunting data collected after the start of trapping were included (Fig. 6, white circles), the model consistently over-predicted the culling rate after about 50 months. The model, simulating continuous hunting, predicted small but consistent numbers of cats culled every month for a year after the last cat was shot in the actual programme. From this, it can be inferred that eradication by hunting alone, even without breaking for winter as was done in 1987 and 1988, would likely have taken months to years longer if trapping and poisoning had not been introduced into the programme.

Discussion

The Spatial Population Abundance Dynamics Engine is a new tool designed to be widely applicable to problems in spatial ecology. While based on the STAR model (McMahon *et al.* 2010), it is more efficient and flexible while overcoming some problems in the published implementation of STAR (see Appendix S5). We made some simple assumptions about the management of the target species along with its biology and behaviour to create a model capable of broadly replicating the spatial effects of removal of feral cats from Marion Island, particularly changes to total population size and general distribution. We were able to make some general predictions by extrapolating the model beyond the available data.

The model was able to predict that a single management approach would probably not have succeeded in an appropriate timeframe in this case. This agrees with evidence from previous eradication programmes: use of several concurrent methods is most successful (Veitch 1985; Beeton & McCallum

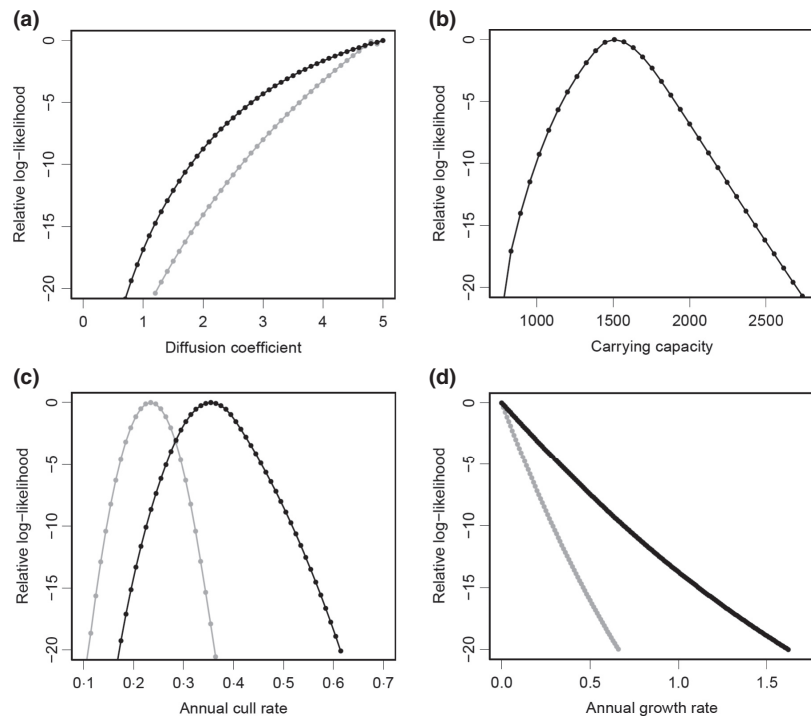


Fig. 2. Profile log-likelihood curves for each of the four free parameters and two goodness-of-fit methods (grey for sighting per effort, black for culling rates), scaled in relation to the global maxima for each curve.

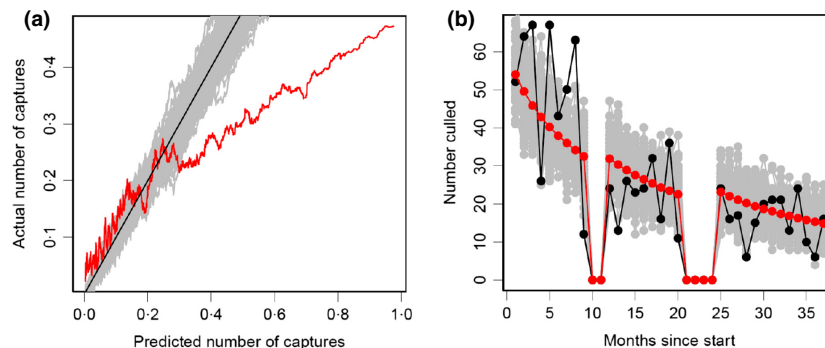


Fig. 3. Illustrations of goodness-of-fit for the best-fitting models using sighting per effort (a) and culling rates (b). Figure (a) contains a 500-sample moving average plot (in red) of the predicted captures per cell using Spatial Population Abundance Dynamics Engine (SPADE) against the observed number, with a black line denoting the ideal 1:1 relationship between predicted and measured results. In (b), the number of predicted culled per month (in red) is contrasted with the number recorded (in black), including months in which no culling took place. Results for both figures are contrasted with 100 examples of simulated data from Poisson distributions based on the SPADE model (in grey).

2011). Although not demonstrated here, SPADE is also able to simulate cases using multiple disparate approaches with different costs, mechanisms (described in Materials and Methods) and levels of effectiveness.

Eradication is not always possible or feasible for large islands (Nogales *et al.* 2004; Oppel *et al.* 2010; Campbell *et al.* 2011) or mainland invasive populations, particularly when complex socioeconomic factors come into play. For such cases, SPADE includes features which allow researchers to build realistic and achievable scenarios for either management or eradication. Like its predecessor (STAR), SPADE includes calculations of management cost and algorithms for cost-benefit optimisation. These incorporate a user-defined spatial priority map based on potential conservation and social benefits or issues involved in managing different regions.

Although we have applied SPADE in a straightforward fashion here for illustration, its flexibility means that it is also capable of modelling far more complex problems involving seasonality, spatially targeted management and even interactions between multiple species and/or age classes within species. One of the most powerful additional features in SPADE is the incorporation of multiple interacting species. This is significant given that management of one species can have cascading effects on the distribution and abundance of others through processes such as mesopredator or prey release (Courchamp, Langlais & Sugihara 1999; Bergstrom *et al.* 2009). Modelling multiple interacting species can also be used for spatial modelling of wildlife disease. Many disease models are expressed as coupled Ordinary Differential Equation (ODE) systems (e.g. the Tasmanian devil *Sarcophilus harrisii*: Beeton & McCallum

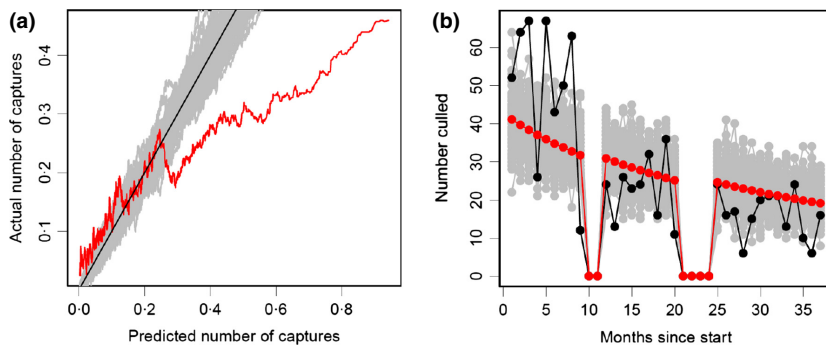


Fig. 4. Illustrations of goodness-of-fit for the best-fitting models where the dispersal rate has been restricted to zero. Sighting per effort (a) and culling rates (b) are represented in the same format as used in Fig. 3 above.

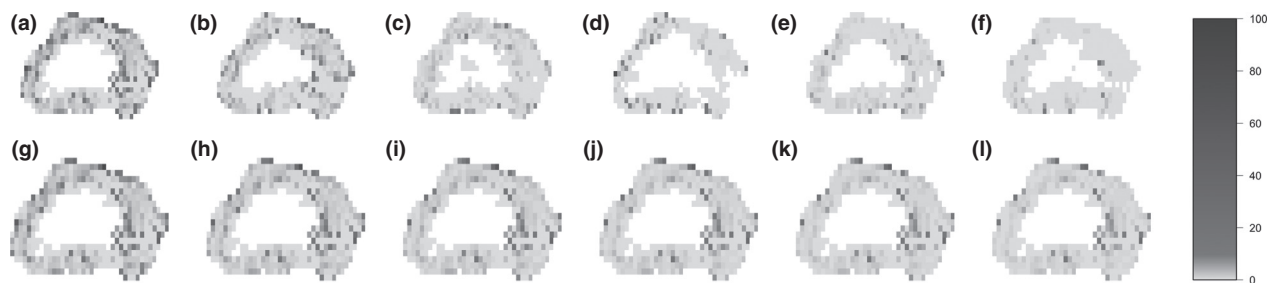


Fig. 5. Comparison of cellwise predicted abundance using the sighting data and trap/sight correction ((a–f), top row) and using the Spatial Population Abundance Dynamics Engine model (g–l, bottom row) with parameters as for the culling model in Table 3 except with the relative cull rate set at 0.3. From left to right, the cells represent average abundance taken over the 1986, 1987, 1988, winter 1989, summer 1989 and 1990 trips, respectively. Darker shades of grey represent higher levels of abundance.

Table 4. Best-fit parameters and maximum log-likelihoods for both goodness-of-fit methods as in Table 3, but where the diffusion coefficient is set to zero

	Diffusion (cats/year)	Carrying capacity	Relative cull rate	Annual growth rate	Maximum log-likelihood
Sighting per effort	0	N/A	0.085	0.000	−7347.9
Culling	0	2005	0.150	0.000	−3096.2

2011; Beeton & Forbes 2012; Beeton 2012, PhD thesis) which can be incorporated into SPADE's modelling framework. These models could potentially be further extended by considering additional species that may be directly or indirectly affected by a disease, such as reservoir hosts, competitors, predators or prey.

Given the variety in current conservation management problems, SPADE was designed specifically with more powerful analyses in mind. The model can be run from R without the user interface, which allows the model runs to be automated using R scripts; the analyses reported here were performed in this way, and the code is available as a template along with the source code for SPADE (see Appendix S4, or download version 0.2.0 at <https://github.com/nickbeeton/SPADE>). The package has been designed to be as flexible as possible for experienced modellers to modify and improve as needed for their own specific purposes.

SPADE has been designed to be as easy to use as practically possible, in particular by users who may not be experienced

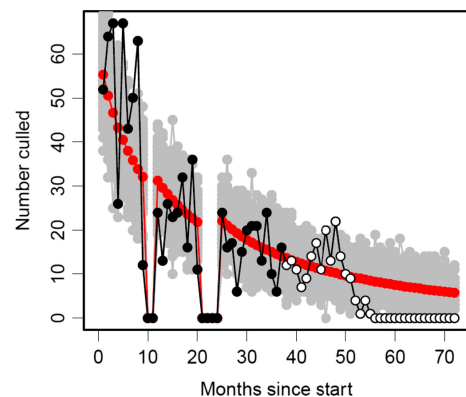


Fig. 6. Modelled (red) with simulated culling rates (grey) vs. actual culling by hunting rate (black before trapping and poisoning, white after trapping and poisoning) for model with parameters set as in Fig. 5.

modellers. Basic scenarios can be run quickly and easily given some spatial and biological information on the target species (e.g. feral deer in Tasmania; Potts *et al.* 2015). One of the potential constraints in using SPADE effectively is having the ability to include environmental layers into the models, although tools are available and others are being developed to assist with this (see in particular MCAS-S; Lesslie *et al.* 2008, and Maxent). However, most conservation agencies contain GIS analytical capability and expertise, which will help overcome this limitation.

Because of its ease of use, SPADE is ideally placed to be part of an adaptive management framework, where data collected during monitoring and management can be iteratively fed back

into the model to test its assumptions and improve its predictive power. As demonstrated in this case study, management plans undertaken with either opportunistic or haphazard monitoring can produce data that is difficult to interpret or analyse. Intensive monitoring and controlled experimental design is often by necessity a secondary consideration in management planning; despite this, it is often worth investing in due to the potential for developing models to help inform later stages of management.

Acknowledgements

The development of SPADE was aided extensively by input from the Australian Alps National Parks Cooperative Management Programme's Feral Horse Working Group, including participants from Parks Victoria, the NSW National Parks and Wildlife Service, the ACT Parks and Conservation Service and Forestry Corporation NSW. We are particularly grateful to Daniel Brown and Charlie Pascoe from Parks Victoria for data and extensive discussions. This work was supported by the Landscapes and Policy Research Hub, which is funded through the Australian Government's National Environmental Research Programme and Kakadu National Park through the Director of National Parks. Finally, the manuscript was improved considerably by thoughtful recommendations from the anonymous reviewers.

Data accessibility

Relevant data and code based on the eradication program has been deposited in the Dryad repository: <http://datadryad.org/resource/doi:10.5061/dryad.q202d>. The R package containing SPADE is available at: <https://github.com/nickbeeton/SPADE> (version 0.2.0 was used in this article).

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Received 22 April 2015; accepted 19 June 2015

Handling Editor: Barbara Anderson

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. SPADE manual.

Appendix S2. Details of algorithms used in SPADE.

Appendix S3. Details of statistical models.

Appendix S4. Source code for SPADE package.

Appendix S5. Description of potential issues in using STAR.