

# To sample or eradicate? A cost minimization model for monitoring and managing an invasive species

Tiffany L. Bogich<sup>1\*</sup>, Andrew M. Liebhold<sup>2</sup> and Katriona Shea<sup>3</sup>

<sup>1</sup>Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK;

<sup>2</sup>Northern Research Station, US Department of Agriculture Forest Service 180 Canfield Street, Morgantown, WV 26505, USA; and <sup>3</sup>Department of Biology, 208 Mueller Laboratory, The Pennsylvania State University, University Park,

PA 16802, USA

## Summary

1. Considerable effort is expended by national and local governments to exclude alien species via detection and eradication of invading populations, but these efforts are not necessarily designed in the most economically or biologically efficient manner.

2. Using the invasion of the European strain of the gypsy moth *Lymantria dispar* into the USA as a case study, we develop an analytical model to determine the optimal trap density for detecting isolated infestations. Most models focus on monitoring or eradication costs only; our model considers the costs of both detection and eradication when determining the best monitoring strategy.

3. The model assumes that all isolated populations must be located and eradicated by the conclusion of a programme. For programmes lasting longer than 1 year, it is more worthwhile to proactively monitor and manage rather than to wait until the programme is over.

4. For a management programme of a given length, optimal trap density is most influenced by the growth rate of the infestation. Optimal trap densities are lowest for infestations with very low growth rates (because they remain small and therefore are less expensive to eradicate) or very high growth rates (because they are easier to detect), and highest for infestations with moderate growth rates (because they are neither inexpensive to eradicate nor easy to detect).

5. Our model is useful in setting a baseline level of monitoring for isolated incidents of gypsy moth invasion. Analysis of data in two US states show that actual trap densities are far higher than the optimal densities from the model. The difference suggests risk aversion may play a role in real systems.

6. *Synthesis and applications.* Our model suggests that we can improve the efficiency of detection and eradication programmes for isolated infestations by optimizing detection effort relative to infestation growth rates and management programme duration. It also clearly demonstrates the importance of balancing the costs and benefits of both detection and eradication when developing invasive species monitoring programmes.

**Key-words:** cost minimization, detection, eradication, gypsy moth, *Lymantria dispar*, pheromone traps, risk aversion

## Introduction

Since Elton's observations initiated the field of invasion biology (Elton 1958), the problem of invasive species control has continued to be a prominent issue. Despite advances in science and technology, biological invasions comprise one of the century's most serious environmental problems (Mack *et al.* 2000). Invasive species threaten economies, societies, and

ecosystems across the globe, costing billions of US dollars per year in increased management costs in addition to the indirect costs of environmental damage, trade disruption, and disease risk (Pimentel *et al.* 2000; GISP 2005; Lodge *et al.* 2006). Considerable effort is currently directed toward the detection and eradication of invasive species in many countries, but these efforts are not necessarily designed in the most economically or biologically efficient manner.

Early intervention is generally considered one of the most cost-effective approaches to reduce the impact of invasive

\*Correspondence author. E-mail: tlb24@cam.ac.uk

species (Myers *et al.* 2000; Byers *et al.* 2002; US NISC 2005). But intervention can only proceed after an alien invasion has been detected; therefore, surveys aimed at detecting incipient invasions are critical. However, practical limitations often constrain the detection and management of small, newly founded alien populations (Welk 2004; Liebhold & Tobin 2006). Monitoring can be expensive, and thus should be considered explicitly when trying to manage invasive pests (Hauser, Pople & Possingham 2006). Therefore, there is an urgent need to design and test joint monitoring and management strategies in order to achieve early detection and, in turn, provide more effective control.

As it may be logistically difficult to conduct experiments to test monitoring strategies, modelling can allow for the evaluation of a variety of monitoring plans before actual implementation in the field (Byers *et al.* 2002). A significant body of literature exists on the design of optimal monitoring strategies (e.g. Nychka & Saltzman 1998; Berliner, Lu & Snyder 1999; Chao & Thompson 2001; Field, Tyre & Possingham 2005; Gerber *et al.* 2005) and also on the design of optimal management strategies (e.g. Milner-Gulland *et al.* 2001; Possingham *et al.* 2001; Tenhumberg *et al.* 2004; Tildesley *et al.* 2006). Only recently have there been efforts to simultaneously consider the costs and benefits of both monitoring and management (Field *et al.* 2004; Yokomizo, Haccou & Iwasa 2004; Gerber *et al.* 2005; Hauser *et al.* 2006), although none of these studies have explicitly addressed the detection/eradication problem.

Consideration of the costs and benefits of both detection and eradication efforts is crucial to determining an overall alien species exclusion strategy. At one extreme, a manager could choose to allocate most funds to monitoring during the course of a multi-year programme, in which case invading populations would be detected when they were very young and small; here, monitoring costs would be high and eradication costs would be low. At the other extreme, a manager could invest very little money in detection, in which case most invading populations would not be detected until they had grown to a larger size; here, monitoring costs would be low but eradication costs would be high. By developing a model that simultaneously considers both detection and eradication costs, we are able to optimize the efficiency of the overall programme and even investigate how this trade-off is affected by programme length, costs, colony growth rate, and the initial infestation density of the species being managed.

In this study, we present a model that captures the trade-off between detection and eradication costs in the design of an optimal monitoring strategy. This model is general and is applicable to most alien species detection/eradication programmes. We demonstrate the model by applying it to invading populations of the gypsy moth *Lymantria dispar* (L.) in western states of the USA.

### Case study: the gypsy moth in North America

The gypsy moth *Lymantria dispar* is native to temperate Eurasia but was accidentally released near Boston in 1869.

Since then, it has gradually expanded its range through eastern North America (Liebhold, Halverson & Elmes 1992). Gypsy moth caterpillars are polyphagous, feeding on over 500 different shrub and tree species; sporadically, populations reach high densities over large regions, resulting in extensive areas of forest defoliation (Elkinton & Liebhold 1990).

Many of the forest types in western North America are suitable for gypsy moth development, but the insect has not become established there because of intensive efforts to detect and eradicate invading populations. Gypsy moth egg masses are often laid on motor vehicles and other objects that are transported from infested areas in the east to uninfested areas in the west. During years when populations in eastern North America are in an outbreak phase, the frequency of these accidental introductions is particularly high (McFadden & McManus 1991). While most of these introductions fail to establish reproducing populations, a few populations do succeed and they form isolated colonies that slowly grow in numbers and gradually expand in their spatial extent (Liebhold & Bascombe 2003; Liebhold & Tobin 2006). Every year, thousands of pheromone-baited traps are placed in uninfested areas in order to detect these isolated colonies. Once colonies are detected, trapping is continued in the area for several years in order to confirm the persistence of the population and spatially delimit the area for eradication (Liebhold & Bascombe 2003). During the last 50 years, over 100 such populations have been detected and eradicated (V. Mastro, personal communication).

### Methods

We developed a spatially implicit model to determine the best trapping density to use with joint management goals of completely eradicating all isolated populations and minimizing programme cost. The model considers an area that is initially devoid of the alien species, and assumes Complete Spatial Randomness (CSR) of both the arrival and establishment of new colonies and the distribution of point surveys (e.g. pheromone traps). CSR assumes that, given a fixed number of events, each event is equally likely and is independent of all other events (Diggle 2003). Although a simplification, CSR is a convenient assumption for a first attempt at modelling this system and is often used as a standard against which others models can be tested.

In the model, the colonies exist as circular regions and their area is proportional to the square of their age multiplied by a growth rate parameter (Skellam 1951; Shigesada & Kawasaki 1997; Sharov, Liebhold & Roberts 1998). If a circular colony overlaps a survey point, then the colony is detected and immediately eradicated. If not, the colony continues to grow. We assume that all colonies must be eradicated during the programme of a given length; otherwise, a cost for detecting and eradicating remaining infestations is incurred.

We assume that colonies arrive in year 0, and monitoring activities commence in year 1, after the colonies have grown. The assumption of a single successful colonization event (with a number of colonies establishing at this time) is appropriate, for example, when a nursery discovers it has shipped infested plants to homeowners but no record was made of where these homeowners live. We assume an initial infestation density of 0.001 colonies per km<sup>2</sup>. This is an average value taken from Sharov *et al.* (1998); actual arrival rates and densities of

new infestations will vary by year and by geographic area, making it essential to test the sensitivity of this parameter, in particular (see below).

Adapting Skellam's (1951) model of spread, Sharov *et al.* (1998) assumed that gypsy moth spread is diffusive and that colony area is proportional to age (time),  $t$ , squared, multiplied by a growth parameter,  $g$ . We used a growth parameter,  $g$ , of  $7.1 \text{ km}^2 \text{ year}^{-2}$  which is an average value, determined from the historical growth of colonies as measured by pheromone trap grids (Sharov *et al.* 1998). The radial colony growth rate per year is the square root of the growth parameter. We assume a random placement of traps, and that colonies are also distributed randomly in space, so that the probability of detection,  $f(g, t, d_t)$ , is equal to one minus the zero term of the Poisson distribution, with mean,  $\lambda = t^2 g d_t$ , dependent on colony area,  $t^2 g$ , and trap density,  $d_t$  (Sharov *et al.* 1998), as given by equation 1. It is the probability of at least one successful colonization event.

$$f(g, t, d_t) = 1 - e^{-(t^2 g d_t)} \quad \text{eqn 1}$$

Using the probability of detection function, we can determine the total area of detected colonies and hence the cost of both the trapping and eradication efforts. Specifically, we calculate four different types of cost: (i) trap cost – the amount spent on trapping activities, (ii) eradication costs – the amount spent on eradication activities, (iii) termination costs – a one-time cost, calculated at the end of the programme, for detecting and eradicating any remaining colonies, and (iv) total cost – the sum of trap, eradication, and termination costs. Termination costs are calculated to meet the model assumption that all infestations must be eradicated within the programme – it is essentially a penalty cost for implementing a programme that did not result in the detection and eradication of all colonies. Costs are presented by year and by total programme length.

We assume that each trap costs \$50, including overhead costs (Mayo, Straka & Leonard 2003), and we determine the cost of trapping for each year,  $C_p$ , to be a linear function of trap density,  $d_t$ , total area,  $A$ , and the cost per trap,  $c_p$  (equation 2).

$$C_p = (A d_t) c_p \quad \text{eqn 2}$$

Assuming that if a colony is detected then it is eradicated, we can calculate the cost of eradication for each year of a programme of length  $T$  (equation 3).

$$C_e = \begin{cases} aA(g t^2) f(g, t, d_t) c_e & t = 1 \\ aA(g t^2) f(g, t, d_t) c_e \prod_{k=1}^{t-1} (1 - f(g, k, d_t)) & 2 \leq t \leq T \end{cases} \quad \text{eqn 3}$$

In the first year, the cost of eradication is the product of the number of colonies that arrive and establish per  $\text{km}^2$ ,  $a$ , the size of the total area in consideration,  $A$ , the size of the infested area,  $(g t^2)$ , the probability that the infested area is detected,  $f(g, t, d_t)$ , and the per-area cost of eradication,  $c_e$ , (equation 3,  $t = 1$ ). For all other years of the programme, eradication cost is calculated in the same fashion, but additionally includes the product of the probability of not detecting colonies in previous years,  $1 - f(g, k, d_t)$  (eqn 3,  $2 \leq t \leq T$ ). Eradication of most isolated gypsy moth populations is carried out via aerial application of the microbial pesticide, *Bacillus thuringiensis*. We assume that the cost of eradication is proportional to infested area (approximately  $\$5000 \text{ km}^{-2}$ ; Sharov *et al.* 1998).

Total cost for year  $t$  of a given programme,  $C_t$ , is then calculated as the sum of eradication and trapping costs for year  $t$  (equation 4).

$$C_t = C_e + C_p \quad \text{eqn 4}$$

**Table 1.** Parameters used in cost equations and baseline values where applicable. The colony growth parameter, eradication cost per infested area, and the initial infestation density were taken from Sharov *et al.* (1998). The cost per trap was taken from Mayo *et al.* (2003)

Parameter	Symbol	Baseline
Colony growth parameter ( $\text{km}^2 \text{ year}^{-2}$ )	$g$	7.1
Eradication cost per infested area ( $\$ \text{ km}^{-2}$ )	$c_e$	5000
Cost per trap ( $\$ \text{ trap}^{-1}$ )	$c_p$	50
Initial infestation density ( $\text{km}^{-2}$ )	$a$	0.001
Total area ( $\text{km}^2$ )	$A$	10 000
Total programme length (years)	$T$	Varies
Time (year)	$t$	Varies
Probability of detection	$f(g, t, d_t)$	Varies
Density of traps (traps $\text{km}^{-2}$ )	$d_t$	Varies
Terminal density of traps (traps $\text{km}^{-2}$ )	$d_T$	Varies

In order to meet the assumption that all colonies are eradicated by the end of the programme, we calculate the cost of eradicating any remaining colonies at what would essentially be the beginning of time  $T + 1$ . This is the termination cost,  $C_m$  (equation 5).

$$C_m = aA(g T^2) c_e \prod_{k=1}^{k=T} (1 - f(g, k, d_t)) + A d_T c_p \quad \text{eqn 5}$$

As it is an extension of eradication and trapping costs, the termination cost is broken into two parts. The first is calculated in the same fashion as  $C_e$ , and the second, in the same fashion as  $C_p$ . For the trapping component, the terminal trap density,  $d_T$ , is the trap density required to ensure that the probability of detection in year  $T$  is 1.00, thus ensuring that the remaining infestation can be found and eradicated. For the eradication component, the product of the probability of not detecting the colonies in previous time steps is calculated over the entire length of the programme.

Total cost for the entire length of the programme,  $C_{\text{total}}$ , is the sum of termination costs for the programme and the total cost for each individual year of a given programme of length  $T$  (equation 6).

$$C_{\text{total}} = C_m + \sum_{t=1}^{t=T} C_t \quad \text{eqn 6}$$

Using baseline parameter values (Table 1), we modelled total costs and the corresponding trapping, eradication, and termination costs for a 5-year management programme. We also determined minimum total costs and corresponding optimal trap densities for programmes up to 20 years in length. Model parameters were tested singly and in critical combinations for sensitivity in the 5-year management programme.

#### PARAMETER SENSITIVITY

In order to determine the effect of the parameters on the optimal trapping density, we performed a sensitivity analysis on the model for a 5-year management programme, by varying one parameter at a time and keeping all other parameters at baseline levels (Table 1). The parameters tested were initial infestation density ( $0.001 \text{ km}^{-1}$ – $1 \text{ km}^{-1}$ ); growth ( $1 \text{ km}^2 \text{ year}^{-2}$ – $20 \text{ km}^2 \text{ year}^{-2}$ ); eradication cost per infested area ( $\$10$ – $\$10\,000$ ); cost per trap ( $\$0$ – $\$10\,000$ ); and total area ( $1 \text{ km}^2$ – $1\,000\,000 \text{ km}^2$ ). We also tested the combined effect of varying programme length (1–10 years) with population growth rate ( $1 \text{ km}^2 \text{ year}^{-2}$ – $20 \text{ km}^2 \text{ year}^{-2}$ ) and of varying programme length

**Table 2.** Optimal trap densities, minimum total cost for the whole programme, and minimum total cost per year for programmes from 1 to 20 years in length for a managed area of 10 000 km<sup>2</sup>. Programme costs are given as a minimum total cost for the entire programme (calculated as the length of the programme times the minimum total cost per year), and as the minimum total cost for each year of the programme. Although the termination cost is a one-off cost incurred at the conclusion of a programme, it is incorporated into the minimum total cost per year by dividing by the programme length

Programme length (years)	Optimal trap density (traps km <sup>-2</sup> )	Minimum total cost (\$)	Minimum total cost per year (\$ year <sup>-1</sup> )
1	0.000	728 500.00	728 500.00
2	0.285	874 284.46	437 142.23
3	0.230	950 044.81	316 681.60
4	0.192	1 036 916.01	259 229.00
5	0.166	1 117 607.17	223 521.43
6	0.147	1 191 152.56	198 525.43
7	0.133	1 258 538.83	179 791.26
8	0.122	1 320 244.61	165 030.58
9	0.114	1 378 105.61	153 122.85
10	0.106	1 432 034.92	143 203.49
11	0.100	1 483 207.10	134 837.01
12	0.095	1 531 608.90	127 634.07
13	0.091	1 577 623.84	121 355.68
14	0.087	1 621 553.42	115 825.24
15	0.083	1 664 149.83	110 943.32
16	0.080	1 704 570.67	106 535.67
17	0.077	1 744 021.08	102 589.48
18	0.075	1 782 085.22	99 004.73
19	0.073	1 818 957.10	95 734.58
20	0.070	1 854 163.08	92 708.15

**Table 3.** Data used to calculate the actual trap density and the infestation density specific to California (CA) and Washington (WA) states in the US. Modelled values are also given for total programme cost (over the entire length of a 5-year management programme) and for the optimal trap density as predicted using the specified arrival rate for each state

State	No. of traps	No. of eradication sites	Years	State area (km <sup>2</sup> )	Actual trap density (traps km <sup>-2</sup> )	Infestation density (km <sup>-2</sup> )	Model total cost (\$)	Optimal trap density (traps km <sup>-2</sup> )
CA	21 321	27	1982–2001	403 973	0.053	0.00000334	1 251 830.00	0.002
WA	24 000	10	2001–2007	172 445	0.139	0.00000828	1 007 723.90	0.008

(1–10 years) with eradication cost per infested area (\$10–\$10 000) on best trapping density. We assumed that cost does not have any impact on effectiveness, (i.e. a more expensive trap does not mean that it is a more effective trap). An increase in trap cost could, however, reflect geographic variations such as labour costs, road density, terrain, vegetation or other factors that affect accessibility to monitoring sites (Mayo *et al.* 2003).

#### OPTIMAL TRAP DENSITIES FOR WEST COAST STATES OF THE U.S.

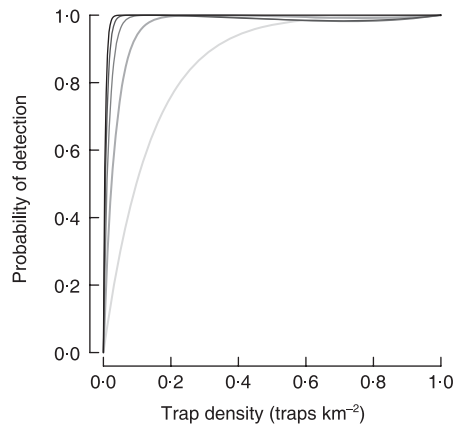
We calculated total programme costs for a sample of trap densities actually used in the field in two western states in the USA and compared the results to the model results for a 5-year programme. In order to apply our model to a specific invasion, information on the invasion history (in terms of eradication efforts over a period of time) and trapping regime (either number of traps or a density of traps) is needed. For two states, California (CA) and Washington (WA), detailed information was available (<http://agr.wa.gov/PlantsInsects/InsectPests/GypsyMoth>, for Washington; C. Pizzo, personal communication, for California). We used our model, with updated parameter information, to determine optimal trap densities for the gypsy moth invasion specific to CA and WA. For each state, the initial infestation density was calculated as the number of eradication sites over the length of time considered, all over the total area of the state (Table 3). Although an estimate, this provides a

more accurate reflection of the infestation density in each state than our baseline value. The total area for CA and WA was then modified to reflect the total land area of each state (US Census Bureau, <http://quickfacts.census.gov/qfd/states>). All other parameters were kept at baseline. We compared the model-predicted optimal trap density with the actual trap density used in each state. Actual trap density for a state is calculated as the number of traps used each year on average divided by the land area of the state.

#### Results

Given the baseline growth parameter (Table 1), the probability of detecting a 1-year-old colony was near 1.00 with a trap density of 2.735 traps km<sup>-2</sup>. Continuing as the colony aged, the probability of detection was near 1.00 at 0.605 traps km<sup>-2</sup> for a 2-year-old colony, at 0.275 traps km<sup>-2</sup> for a 3-year-old colony, at 0.155 traps km<sup>-2</sup> for a 4-year-old colony, and at 0.105 traps km<sup>-2</sup> for a 5-year-old colony (Fig. 1).

Figure 2 illustrates how the minimum costs and optimal trap densities are selected for a 5-year management programme; results were similar for other programme durations. The best trap density was 0.166 traps km<sup>-2</sup>, and was determined as the trap density corresponding to the minimum total cost. In a similar fashion, we determined the minimum programme costs (Fig. 3A), minimum total costs per year (Fig. 3B), and

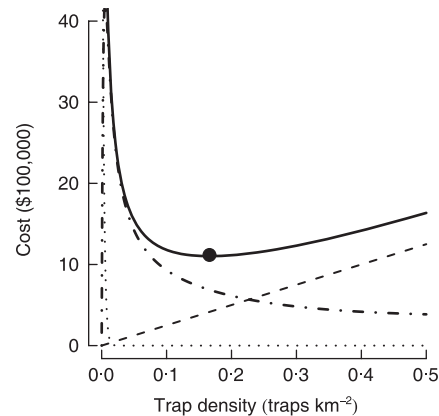


**Fig. 1.** The probability of detection function,  $f(g, t, d_i)$  plotted against trap density for colonies of age 1 to 5, detailed by lines of increasing shades of grey from light grey for colonies of age 1 to black for colonies of age 5. Year 1 colonies (lightest grey line) are the smallest and, therefore, most difficult to detect, and year 5 colonies (black line) are the largest and easiest to detect.

the corresponding best trap densities (Fig. 3C) for programmes of 1 to 20 years in length. Values for the minimum total and per-year programme costs and the corresponding best trap density for each programme length are given in Table 2. As programme length increased, the trapping density needed to ensure complete eradication while minimizing cost decreased (Fig. 3C), and the minimum programme cost per year decreased as well (Fig. 3B). Longer programmes, however, had greater total costs than shorter programmes when per annum costs are summed (Fig. 3A). Termination costs were only significant for 1-year programmes.

#### PARAMETER SENSITIVITY

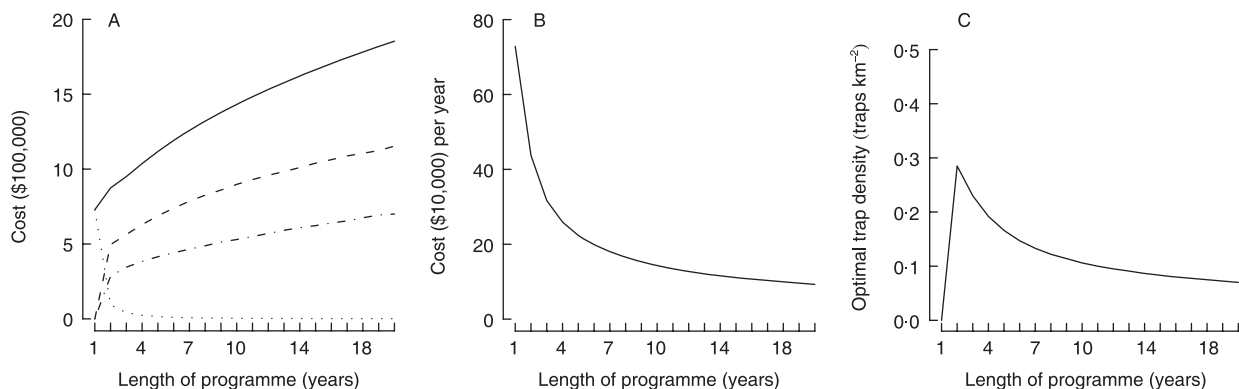
For the initial infestation density, the most significant changes in optimal trap density occurred for infestation densities between 0.001–0.021  $\text{km}^{-2}$  (Fig. 4A). Further increase of infestation densities resulted in an increase in optimal trap density, but at slower increments. For growth rates of 1–10  $\text{km}^2 \text{year}^{-2}$ ,



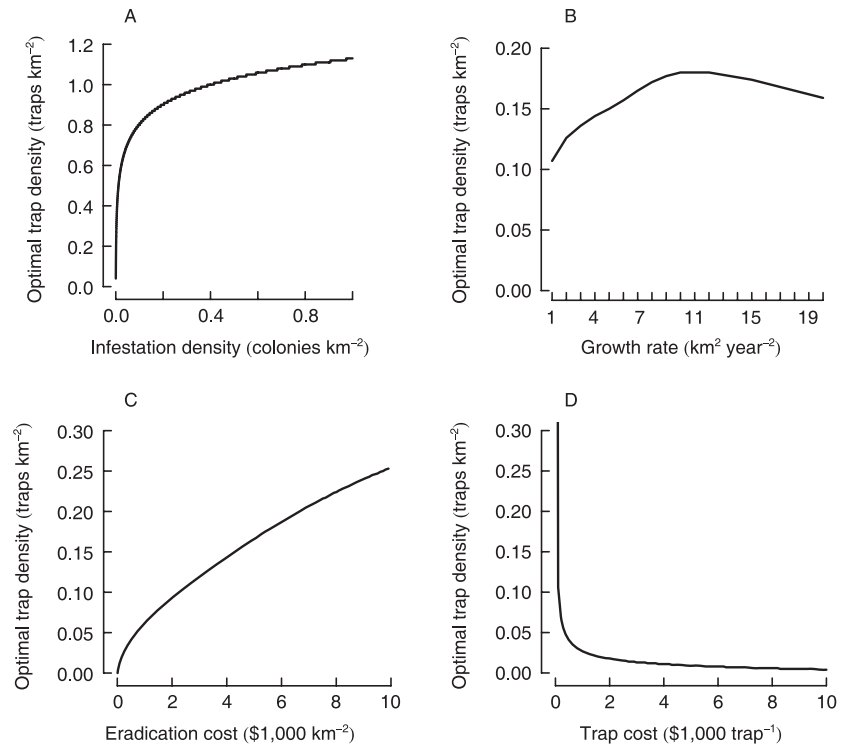
**Fig. 2.** Total costs (solid line), eradication costs (dash-dotted line), trapping costs (dashed line), and termination costs (dotted line) against trap density are given for a 5-year management programme. The trap density corresponding to the minimum total cost is optimal, and is denoted by a point on the total cost line.

optimal trap density increased from 0.107–0.180 traps  $\text{km}^{-2}$ ; for higher growth rates, optimal trap density decreased again, but not as rapidly (Fig. 4B). As the eradication cost per  $\text{km}^2$  increased, optimal trap density increased as well (Fig. 4C). For per-trap costs approaching \$0, the optimal trap density asymptoted to infinity, as there was no limitation to trapping (Fig. 4D). As the cost per trap increased, the optimal trap density quickly decreased and approached extremely low densities. Note that total area had no influence on optimal trap density.

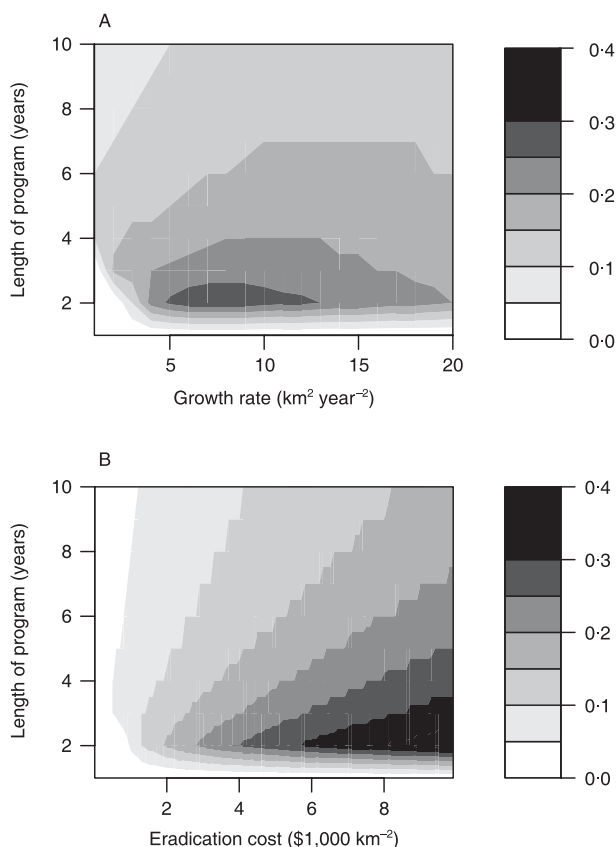
The combined effects of programme length and either growth rate or eradication cost per  $\text{km}^2$  on optimal trap density are shown in Fig. 5. For low growth rates, optimal trap densities were low; for moderate growth rates, optimal trap densities were higher; for high growth rates, trap densities were again lower. The highest optimal trap densities occurred for 2-year programmes, with colony growth rates between 5  $\text{km}^2 \text{year}^{-2}$  and 13  $\text{km}^2 \text{year}^{-2}$  (Fig. 5A). For programmes of any length, when eradication costs per  $\text{km}^2$  were low, then the optimal trap density was also low or zero (Fig. 5B). As eradication cost



**Fig. 3.** For programmes of 1 to 20 years duration, (A) minimum overall total (solid line), eradication (dashed line), trapping (dash-dotted line), and termination (dotted line) costs, (B) the minimum total programme cost per year, and (C) the optimal trap densities are given.



**Fig. 4.** Parameter sensitivity showing the effect of varying each parameter individually on the optimal trap density for a 5-year management programme. Plots are shown for (A) initial infestation density, (B) colony growth rate, (C) eradication cost per km<sup>2</sup>, and (D) cost per trap.

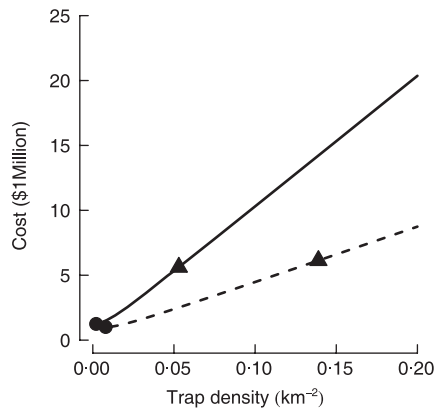


increased, optimal trap density also increased; the highest optimal trap density occurred for 2-year programmes with the highest eradication cost per km<sup>2</sup>. On average, optimal trap density was lower for longer programmes, regardless of other parameter values.

#### OPTIMAL TRAP DENSITIES FOR WEST COAST STATES OF THE USA

We determined how our model-predicted optimal trap density compared to actual trap densities used to monitor the gypsy moth in two states, California (CA) and Washington (WA), where the species has not yet established. Using the model for a 5-year management programme with realistic infestation densities and total areas for each state (Table 3), we calculated the total 5-year programme cost corresponding to trap densities from CA and WA (Fig. 6). The model-predicted optimal trap density was lower than the actual trap density for both states. Infestation density was much lower than the baseline value and the total area was much larger than the baseline area (Tables 1 and 3); thus, the relationship of total

**Fig. 5.** Contour plots of the effect of varying (A) programme length and growth rate and (B) programme length and eradication cost per km<sup>2</sup> on optimal trap density. Higher optimal trap densities are given by darker shades of grey.



**Fig. 6.** Overall total programme costs against trap density for 5-year management programmes in California (solid line) and Washington (dashed line), as predicted by the model, using an initial infestation density and total area specific to each state. The optimal predicted trap density is given by a solid circle, and the actual trap density is given by a solid triangle.

cost to trap density was dominated by an increase in cost with increase in trap density above the low, optimal trap density. This increase was sharpest for California (Fig. 6; solid line).

## Discussion

Our model identifies the optimal density of pheromone traps that will minimize programme costs while accounting for the trade-off between investing in monitoring versus management activities required to successfully eradicate isolated outbreaks of the invasive gypsy moth. We have shown the importance of considering both trapping and eradication when developing a monitoring programme and that the optimal trap density depends strongly on both biological aspects (initial infestation density and colony growth rate) and on economic parameters (such as the programme length, trap costs, and per-area eradication costs). This model can easily be updated with other details relevant to this species as they arise, and can also be applied to other invasive species.

The inclusion of the termination cost was used as a way to penalize programmes that did not eradicate all colonies within the length of the programme. Interestingly, all programmes, aside from the 1-year programme, had insignificant termination costs. This demonstrates that it is worthwhile to proactively monitor and manage, rather than wait until the end of the programme.

The optimal trap density needed to ensure early detection and eradication is higher for shorter programmes. The only exception is for a 1-year programme in which a lower trapping effort is the least expensive option since eradicating the colonies remaining at the end of the programme is fairly inexpensive (i.e. termination costs are low) as the colonies are still small. The optimal trap density is highest for the 2-year programme (Fig. 3C). This is because it is better to detect and eradicate all colonies during the programme, rather than waiting until after the programme to incur termination costs, so monitoring effort is very concentrated in time. However,

although longer programmes cost less per year (Fig. 3B), they are actually more expensive in terms of overall total programme costs (Fig. 3A).

To further demonstrate the effect of programme length on cost, we examined the difference between the ‘worst-case cost’ (no action is taken until the end of the programme), and the ‘best-case cost’ (all colonies are detected and eradicated in the first year of the programme). The best-case cost is assessed at the end of year 1 and is therefore the same for all programme lengths. The worst-case cost depends on the programme length and increases as programme length increases and colonies are allowed to grow. The result was intuitive: it is always less expensive to detect and eradicate all colonies within the first year of a management programme, and the difference in cost between the best- and worst-case scenarios becomes greater as programme length increases.

When parameter values were varied, the only non-monotonic relationship (hump-shaped function) was obtained for the relationship between optimal trap density and colony growth rate (Fig. 4B). For low growth rates, optimal trap densities were low. When growth rates are low, colonies remain smaller for longer, and are thus cheaper to eradicate. For the high growth rates, optimal trap densities were also low; colonies grow rapidly and are easier to find, and hence a lower trap density can be used without sacrificing detectability. Thus, the reason for the low trap density is related to management for slow-growing colonies (due to cheaper eradication) and to monitoring for fast-growing colonies (due to easier detection). The trade-off between monitoring and management, and the importance of modelling the two together, is demonstrated best by the case of intermediate growth rates. Optimal trap densities are highest for intermediate growth rates because, at these rates, colonies are neither inexpensive to eradicate nor easy to detect. When growth rates are shown in combination with varying programme lengths, this result is particularly evident for short-term management programmes (Fig. 5A).

Other parameters of interest include the density of the initial infestations, the unit cost of eradication and the cost per trap. As the density of initial arrivals is increased, the optimal trap density initially increases rapidly and then asymptotes (Fig. 4A). As eradication becomes more expensive to implement, the optimal trap density increases; regardless of programme length, it becomes imperative to detect colonies when they are smaller and less expensive to eradicate (Figs 4C and 5B). When trapping costs are very low, optimal trap densities are high, as it is inexpensive to increase trapping to a point where detection is nearly certain and eradication costs can be kept low. And, as the cost per trap increases, optimal trap density quickly drops to a low level (Fig. 4D).

Our approach is a first attempt to model monitoring and management together for a pest eradication scenario. There are some obvious possible extensions. For example, we assumed a single colonization event (albeit at a range of infestation densities) at the start of the programme, coinciding with either known introduction episodes or years with large east coast outbreaks. For many species and scenarios, arrivals may occur every year; the model would then need to incorporate continuous

colonization, with varying rates of arrival and establishment. With multiple invasion pulses, the 1-year programme would certainly no longer be appropriate.

Another consideration for future research is the issue of spatial- and temporal-autocorrelation of both trap placement patterns and colony distribution. In some areas of the USA, traps are placed in an irregular fashion, while in other areas, traps are placed in a regular, gridded fashion, with trap spacing varying from finely (1 km) to coarsely (20 km) spaced. The most effective trap spacing has not yet been determined. If the colonies are distributed with complete spatial randomness, the distribution of traps (random vs. non-random) should not change the results. However, if colony formation is not random, then the effect of different trap distributions could either be explored through spatial simulations (Skarpaas, Shea & Bullock 2005) or by using model-based design approaches, where the dynamics of the system are used to make informed sampling design decisions (Muller 1999; Wikle & Royle 1999, 2005). In fact, incorporating more spatial and temporal knowledge, or specifically incorporating learning about the system, may lead to more effective and cost efficient management programmes in general. This can be achieved either by such model-based dynamic design approaches (Muller 1999), or alternatively, by using an adaptive management framework, which includes a specific plan for learning about the system in the management approach (Walters 1986; Williams, Nichols & Conroy 2002).

Comparing our optimal trap density results from the model with actual trap densities used in the field, we determined that our model's results fall into a realistic range of trap densities (Fig. 6), and used the comparison to highlight issues to incorporate into the model in the future. For both CA and WA, the model predicted a lower optimal trap density than that which is currently used, on average, in each state. Three possible explanations for the higher-than-optimal trapping exist: (i) continuous colonization, (ii) spatial and temporal autocorrelation, and (iii) risk aversion. First, the model assumes a single pulse of invasion at the onset of the programme coinciding with eastern population peaks or an isolated shipment of infested material, for example. In reality, new infestations may occur many times throughout a management programme, albeit at very low rates, thus requiring higher levels of trapping than predicted. Secondly, there may be spatial or temporal autocorrelation in both trapping pattern and colony distribution. The founding of isolated gypsy moth colonies is more probable in areas where human population presence is coupled with the presence of suitable host plants. Trap placement may target such areas and traps are also more likely to be placed in areas accessible by road.

A third possible explanation for a higher actual trap density is that the governmental/state authorities are motivated to take action to avoid having to treat large areas. There may be some level of risk aversion in regards to detecting (and eradicating) new gypsy moth invasions as an uncontained infestation of gypsy moth would be catastrophic for western US forests and could result in quarantines that would have significant adverse economic impacts. Large areas are

troublesome because it is more difficult to achieve complete eradication, and treating a larger area would affect a greater number of people. Therefore, there is a very real, but difficult to quantify, benefit to trapping at higher-than-optimal densities in order to avoid the risk of having to treat larger areas. The model shows it is actually less costly to err on the side of higher-than-optimal trapping; the total cost curves (Fig. 2), show a much steeper rise for trap densities below than above optimal. When uncertainty is accounted for in the decision-making process, the most robust decision is the one in which the possibility of an undesired outcome is the lowest (Regan *et al.* 2005).

Through the development of a simple analytical model, the importance of incorporating both monitoring and management when making decisions in regards to either monitoring or management is clear. In the case of the invasion of the gypsy moth, the growth rate of colonies best illustrated the trade-off dynamics between monitoring (trap density) and management (eradication). Slow-growing colonies are cheaper to eradicate whereas fast-growing colonies are easier to detect; both require lower optimal trap densities. On the other hand, intermediate-growing colonies are neither cheap to eradicate nor easy to detect and therefore require higher optimal trap densities. With the examples of gypsy moth programmes in CA and WA, we have shown the applicability of this model to real problems. Continuing to develop models to investigate best monitoring procedures, while also incorporating the costs and benefits of management, will help to significantly improve the efficiency and cost-effectiveness of current gypsy moth programmes. Further, it is our hope that this model can be used as a starting point to developing monitoring and management programmes for other invasive species.

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## References

- Berliner, L.M., Lu, Z.Q. & Snyder, C. (1999) Statistical design for adaptive weather observations. *Journal of the Atmospheric Sciences*, **56** (15), 2536–2552.
- Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology*, **16** (3), 630–640.
- Chao, C.T. & Thompson, S.K. (2001) Optimal adaptive selection of sampling sites. *Environmetrics*, **12** (6), 517–538.
- Diggle, P.J. (2003) *Statistical Analysis of Spatial Point Patterns*, 2nd edn. Arnold, London.
- Elkinton, J.S. & Liebhold, A.M. (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–596.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Field, S.A., Tyre, A.J., Jonzen, N., Rhodes, J.R. & Possingham, H.P. (2004) Minimizing the cost of environmental management decisions by optimizing statistical thresholds. *Ecology Letters*, **7** (8), 669–675.
- Field, S.A., Tyre, A.J. & Possingham, H.P. (2005) Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management*, **69** (2), 473–482.



- Gerber, L.R., Beger, M., McCarthy, M.A. & Possingham, H.P. (2005) A theory for optimal monitoring of marine reserves. *Ecology Letters*, **8** (8), 829–837.
- GISP (2005) Tackling the growing spread of invasive species across the globe: renewed commitment from key international organisations. Global Invasive Species Programme. In: *GISP News*, **4**, 4–5.
- Hauser, C.E., Pople, A.R. & Possingham, H.P. (2006) Should managed populations be monitored every year? *Ecological Applications*, **16** (2), 807–819.
- Liebhold, A. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6** (2), 133–140.
- Liebhold, A., Halverson, J.A. & Elmes, G.A. (1992) Gypsy moth invasion in North America: a quantitative analysis. *Journal of Biogeography*, **19** (5), 513–520.
- Liebhold, A.M. & Tobin, P.C. (2006) Growth of newly established alien populations: comparison of North American gypsy moth colonies with invasion theory. *Population Ecology*, **48** (4), 253–262.
- Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Riechard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T. & McMichael, A. (2006) Biological invasions: recommendations for U.S. policy and management. *Ecological Applications*, **16** (6), 2035–2054.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10** (3), 689–710.
- Mayo, J.H., Straka, T.J. & Leonard, D.S. (2003) The cost of slowing the spread of the gypsy moth (Lepidoptera: Lymantriidae). *Journal of Economic Entomology*, **96** (5), 1448–1454.
- McFadden, M.W. & McManus, M.L. (1991) An insect out of control? The potential for spread and establishment of the gypsy moth in new forest areas in the United States. *Forest Insect Guilds: Patterns of Interactions with Host Trees* (eds Y.N. Baranchikov, W.J. Mattson, F.P. Hain & T.L. Payne), pp. 172–186. US Department of Agriculture Forest Service. General Technical Report NE 153.
- Milner-Gulland, E.J., Shea, K., Possingham, H., Coulson, T. & Wilcox, C. (2001) Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation*, **4**, 157–167.
- Muller, P. (1999) Simulation-based optimal design. *Bayesian Statistics 6: Proceedings of the Sixth Valencia International Meeting 6–10 June 1998* (eds J.M. Bernardo, J.O. Berger, A.P. Dawid & A.F.M. Smith), pp. 459–474. Oxford University Press, Oxford, UK.
- Myers, J.H., Simberloff, D., Kuris, A.M. & Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution*, **15** (8), 316–320.
- Nychka, D. & Saltzman, N. (1998) Design of air-quality monitoring networks. *Case Studies in Environmental Statistics* (eds D. Nychka, W.W. Piegorsch & L.H. Cox), Vol. 132, pp. 51–76. Springer, New York.
- Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50** (1), 53–65.
- Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. & Pulliam, H.R. (2001) Making smart conservation decisions. *Conservation Biology: Research Priorities for the Next Decade* (eds M.E. Soule & G.H. Orians), p. 307. Island Press, Washington, D.C.
- Regan, H.M., Ben-Haim, Y., Langford, B., Wilson, W.G., Lundberg, P., Andelman, S.J. & Burgman, M.A. (2005) Robust decision-making under severe uncertainty for conservation management. *Ecological Applications*, **15** (4), 1471–1477.
- Sharov, A.A., Liebhold, A.M. & Roberts, E.A. (1998) Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) in North America. *Journal of Economic Entomology*, **91** (1), 165–174.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, UK.
- Skarpaas, O., Shea, K. & Bullock, J.M. (2005) Optimizing dispersal study design by Monte Carlo simulation. *Journal of Applied Ecology*, **42** (4), 731–739.
- Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.
- Tenhuberg, B., Tyre, A.J., Shea, K. & Possingham, H.P. (2004) Linking wild and captive populations to maximize species persistence: optimal translocation strategies. *Conservation Biology*, **18** (5), 1304–1314.
- Tildesley, M.J., Savill, N.J., Shaw, D.J., Deardon, R., Brooks, S.P., Woolhouse, M.E.J., Grenfell, B.T. & Keeling, M.J. (2006) Optimal reactive vaccination strategies for a foot-and-mouth outbreak in the UK. *Nature*, **440** (7080), 83–86.
- US NISC (2005) *Progress Report on the Meeting the Invasive Species Challenge: National Invasive Species Management Plan*. US National Invasive Species Council, Beltsville, MD, USA.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Macmillan Publishing Company, New York.
- Welk, E. (2004) Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: purple loosestrife (*Lythrum salicaria*) in North America. *Ecological Modelling*, **179** (4), 551–567.
- Wikle, C.K. & Royle, J.A. (1999) Space-time dynamic design of environmental monitoring networks. *Journal of Agricultural Biological and Environmental Statistics*, **4** (4), 489–507.
- Wikle, C.K. & Royle, J.A. (2005) Dynamic design of ecological monitoring networks for non-Gaussian spatio-temporal data. *Environmetrics*, **16** (5), 507–522.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego, CA, USA.
- Yokomizo, H., Haccou, P. & Iwasa, Y. (2004) Multiple-year optimization of conservation effort and monitoring effort for a fluctuating population. *Journal of Theoretical Biology*, **230** (2), 157–171.

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