

REPORT

The Allee effect, stochastic dynamics and the eradication of alien species

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Abstract

Previous treatments of the population biology of eradication have assumed that eradication can only be achieved via 100% removal of the alien population. However, this assumption appears to be incorrect because stochastic dynamics and the Allee effect typically contribute to the extinction of very low-density populations. We explore a model that incorporates Allee dynamics and stochasticity to observe how these two processes contribute to the extinction of isolated populations following eradication treatments of varying strength (percentage mortality). As a case study, we used historical data on the dynamics of isolated gypsy moth, *Lymantria dispar*, populations to fit parameters to this model. The parameterized model was then used in simulations that evaluated the efficacy of various eradication strategies. The results indicated that eradication of isolated gypsy moth populations could be easily achieved following a treatment of >80% mortality as long as populations were relatively low (indicated by <100 males captured in pheromone traps).

Keywords

Biological invasion, establishment, extinction, gypsy moth, *Lymantria dispar*, population dynamics.

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INTRODUCTION

Recent increases in world trade and travel have caused acceleration in the arrival of alien species. While most alien species have relatively few effects, many species have caused catastrophic ecological impacts (Liebhold *et al.* 1995; Vitousek *et al.* 1996; Parker *et al.* 1999; Simberloff *et al.* 2000). As the problem of alien species escalates, more work is urgently needed on methods to mitigate these problems.

Any invasion proceeds through three distinct phases: arrival, establishment and spread (Dobson & May 1986; Williamson 1996). Corresponding to each of these phases is an approach to managing invasions: quarantine, eradication and containment (Liebhold *et al.* 1995). All three approaches represent important components of an overall strategy to management of biological invasions. However, we restrict our study here to the design of strategies for eradication.

Eradication refers to the total elimination of a species from a geographical area. There is currently considerable interest in eradication both because of the increasing numbers of invasion events and frequent scepticism as to whether eradication is a feasible goal (Perkins 1989; Myers *et al.* 1998; Myers *et al.* 2000; Simberloff 2001). While there

has been extensive exploration of the societal issues associated with eradication programmes, there has been remarkably little exploration of the scientific basis of eradication. In this paper, we apply basic concepts from the population biology of invading populations and apply them to the design of eradication strategies.

Examples of large efforts to eradicate alien plant and animal species include both those that succeeded and others that failed (Dahlsten *et al.* 1989; Myers *et al.* 1998; Myers *et al.* 2000). In most cases, eradication is achieved via destruction of individuals of the alien species (e.g. manual removal of plants, spraying of pesticides, etc.). While the concept of eradication has been applied for many years, little effort has been made to understand the mechanisms by which eradication occurs. One concept that dominates virtually all previous papers on alien pest eradication is the notion that eradication can only be achieved via removal of 100% of the population (Knipling 1966, 1979; Dahlsten *et al.* 1989; Myers *et al.* 1998). For example Dahlsten *et al.* (1989) contrasted costs of eradication with that of ordinary pest management by stating, ‘...cost usually escalates with the last 1% or so, usually requiring a very costly effort as the eradication effort seeks to achieve 100 percent kill.’ In

contrast to the literature on eradication, researchers interested in conservation biology have made considerable progress in understanding the population biology of low-density populations and their extinction (e.g. Lande 1993; Nee 1994). This research has identified at least two processes affecting very low-density populations that are pertinent to extinction via eradication: (1) stochastic variation in dynamics and (2) the Allee effect.

Random processes affect the dynamics of virtually all populations. However two different types of stochastic effects are generally recognized: demographic and environmental stochasticity (Lande 1993). Demographic stochasticity is caused by chance realizations of individual probabilities of death and reproduction in finite populations. As these individual events average out, demographic stochasticity is only important in small populations. Environmental stochasticity arises from a nearly continuous series of random perturbations that similarly affect birth and death rates of all individuals in a population and is important to both large and small populations. Both types of stochasticity can contribute to population extinction when populations are at very low densities (Lande 1993; Stephan & Wissel 1994; Lande *et al.* 1998; Fieberg & Ellner 2001).

The 'Allee effect' was first described by Allee and colleagues (Allee *et al.* 1949) and refers to any process whereby any component of individual fitness is correlated with population size (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Stephens *et al.* 1999). Studies of population dynamics focus on changes in population density rather than on components of fitness and therefore these studies emphasize what Stephens *et al.* (1999) refer to as the 'demographic Allee effect' – the correlation of population size with per capita growth rate. While most instances of Allee effects have been described in low-density populations, these effects may also influence a wide range of densities (Stephens *et al.* 2002). There are a multitude of mechanisms that can cause this type of density dependence in plant and animal populations, especially at low densities. These mechanisms include failure to locate mates, inbreeding depression, failure to satiate predators, and lack of co-operative feeding (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Stephens *et al.* 1999). In many cases, this pattern of decreasing per capita growth with decreasing density includes negative growth at very low densities and populations may thereby decline to extinction. The importance of Allee dynamics in extinction has received considerable attention in studies relating to the conservation of endangered species (Lande 1988; Groom 1998) and to a lesser extent in studies of range expansion during biological invasions (Lewis & Kareiva 1993; Keitt *et al.* 2001). Recent work indicates that the combined influence of Allee

dynamics and stochastic processes strongly influences the successful establishment of alien species (Haccou & Iwasa 1996; Fagan *et al.* 2002; Petrovskii *et al.* 2002).

In this paper, we evaluate how stochasticity and Allee dynamics may influence the effectiveness of various eradication strategies. Specifically, we use a simulation model to observe how the timing and strength of eradication treatments affect eradication success given various levels of stochasticity and Allee dynamics. These simulations provide guidelines for eradication of isolated populations but are not applicable to eradication of widely distributed species. We demonstrate the biological realism of this modelling approach using historical data on the dynamics of isolated gypsy moth, *Lymantria dispar* (L.), populations in North America, and make specific predictions regarding their eradication.

MODELLING INVADING POPULATIONS

Allee dynamics can be caused by a variety of mechanisms. Among these, we can expect virtually all sexually reproducing organisms to exhibit some decline in per capita growth with decreasing density at low densities as a consequence of failure to find mates. Some species may exhibit even stronger Allee dynamics (e.g. as a result of predator satiation) while others species (e.g. asexually reproducing plants) may exhibit no Allee effect.

Several previous studies (Dennis 1989; Amarasekare 1998; Keitt *et al.* 2001) have modified a Verhulst-Pearl 'logistic' growth model to incorporate Allee dynamics. The discrete-time version of this type of model for organisms with non-overlapping generations can be written:

$$\ln(r_t) = \gamma \left(1 - \frac{x_t}{K}\right) \left(\frac{x_t - C}{K}\right), \quad (1)$$

where x is the population density, $r_t = x_{t+1}/x_t$ (change in population density), γ the 'intrinsic rate of natural increase', K the 'carrying capacity', and C the threshold population size below which $r_t < 1$ because of Allee dynamics.

Figure 1(a) shows the form of the simple logistic model and the model incorporating an Allee effect. In both the logistic model and the model incorporating Allee dynamics, K is a stable equilibrium such that when $x_t > K$, populations will decline and when $x_t < K$, populations will increase. However in the model incorporating an Allee effect, C is an unstable equilibrium such that when $x_t > C$ populations will increase, but when $x_t < C$, populations will decrease towards extinction.

When populations are very low, x_t is insignificant compared with K and the term $(x_t/K) \approx 0$. Thus, eqn 1 becomes:

$$\ln(r_t) = \gamma \left(\frac{x_t - C}{K} \right) \tag{2}$$

$$= \frac{-C\gamma}{K} + \frac{\gamma}{K} x_t. \tag{3}$$

Therefore, at very low densities, the Allee effect can be represented simply by $\ln r_t$ as a linear function of x_t with intercept $-C\gamma/K$ and slope γ/K . Decreasing population densities as a result of an Allee effect will thus only occur when $-C\gamma/K < 0$, which occurs when $C > 0$. Thus the magnitude of C is related to the extent to which Allee effects contribute to extinction.

We can further modify eqn 2 to include the effects of additive environmental ‘noise’ that affects the log replacement rate:

$$\ln(r_t) = \gamma \left(\frac{x_t - C}{K} \right) + \varepsilon_t, \tag{4}$$

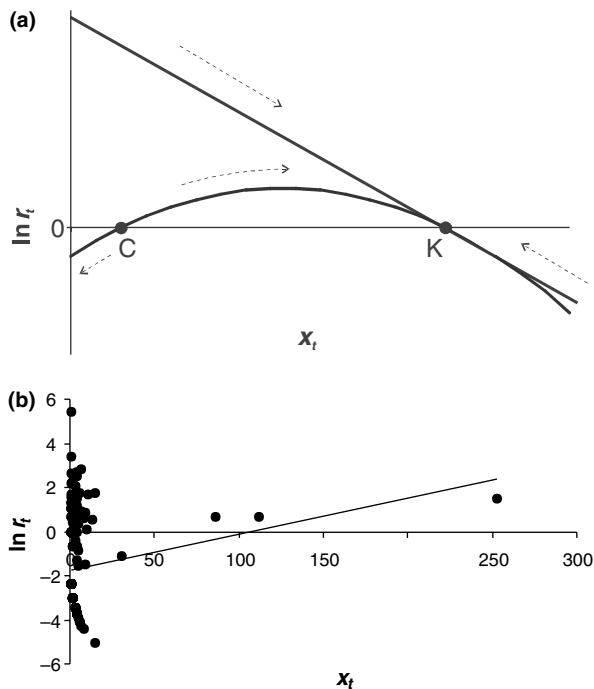


Figure 1 Plots of log per capita growth rate vs. density. (a) Illustration of the discrete form of the logistic model (straight line) and logistic model incorporating an Allee effect (curved line; eqn 1). Arrows indicate the movement of populations towards the stable equilibrium, K , and away from the unstable equilibrium, C . (b) Gypsy moth colony data; each dot represents values for a single colony in a given year. Line is the linear regression model fit to the data.

where ε_t is a random variable with a mean of zero and a SD of σ .

We explored the interaction of environmental stochasticity and Allee dynamics via simulations using eqn 4. All simulations began with an initial ‘inoculation’ of five individuals and eqn 4 was applied to simulate growth from x_t to x_{t+1} . Simulations were run for values of the extinction threshold, C , varying from -5 to 15 and ‘noise’, σ , varying from 0 to 2 . Negative values of C represent the presence of a weak Allee effect that does not cause a decrease in population growth because $\ln r_t > 0$ for all biologically realistic (positive) values of x_t . In all simulations we arbitrarily set $\gamma/K = 0.1$. At the end of 20 generations, any population where $x < 1$ was considered extinct; populations were considered established as long as $x \geq 1$.

Results of these simulations are shown in Fig. 2. In the absence of noise ($\sigma = 0$), there was a sharp cut-off value of $C = 5$, below which all populations established and above which no populations established. This is because, in the absence of noise, the Allee equilibrium C is the threshold, above which populations will always increase and below which populations will always go extinct (Fig. 1). As all simulations began with an initial inoculum of five, values of C below the inoculum always resulted in establishment but C above the inoculum level, always resulted in extinction. As noise was added to the system (increasing values of σ), the relationship between the Allee threshold, C , and establishment generally remained the same except that as stochasticity increased, the transition between 100% establishment and 100% extinction transformed from an abrupt shift to a continuous transition. When an Allee threshold was absent ($C < 0$), establishment always occurred as long as

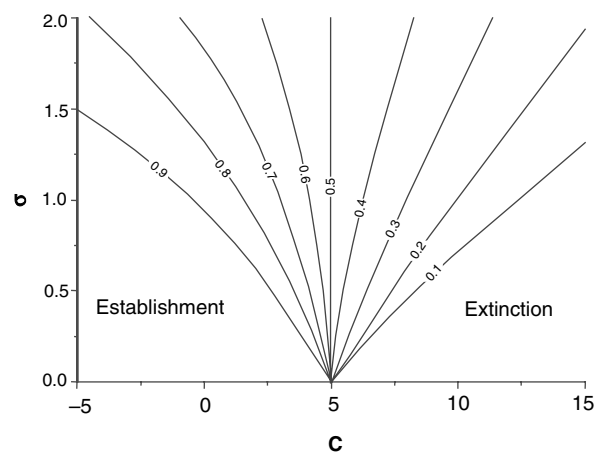


Figure 2 Simulated establishment probabilities 20 generations after inoculation, estimated from 10 000 simulations of eqn 4 under varying levels of the extinction threshold, C , and noise, σ ($x_0 = 5$, $\gamma/K = 0.1$).

stochasticity was zero or very low. But as stochasticity increased, the probability of extinction increased, even for values of $C < 0$. These results demonstrate that extinction may occur either as the result of stochasticity or Allee effects acting on their own or in combination. When the initial inoculum is below the Allee threshold, stochasticity functions to increase the probability of establishment. However, when the inoculum is above the Allee threshold, stochasticity serves to decrease the probability of establishment.

SIMULATION OF ERADICATION TREATMENTS

We next used eqn 4 to simulate the results of eradication treatments applied to the population. The eradication treatments simulated were intended to represent any practice (e.g. application of an insecticide or herbicide, or manual removal of individuals) that kills a given proportion of the population and is applied against a single generation. Population simulations were conducted as described above but modified by applying a kill rate, ϕ (the simulated control measure), at generation, T . We conducted simulations using values of T varying from 1 to 10 and ϕ varying from 0 to 100%.

Figure 3 depicts simulation results (represented by establishment rates) for simulations that were conducted using an inoculum = 5, $C = 5$, $\gamma/K = 0.1$ and $\sigma = 1.0$. These parameter values were selected because they were roughly in the middle of the parameter space used in Fig. 2 and would be expected to produce an establishment rate of 0.5, when no eradication treatment was applied. Results indicate that over most of the values of ϕ and T , there was little reduction in establishment probability (Fig. 3). That is,

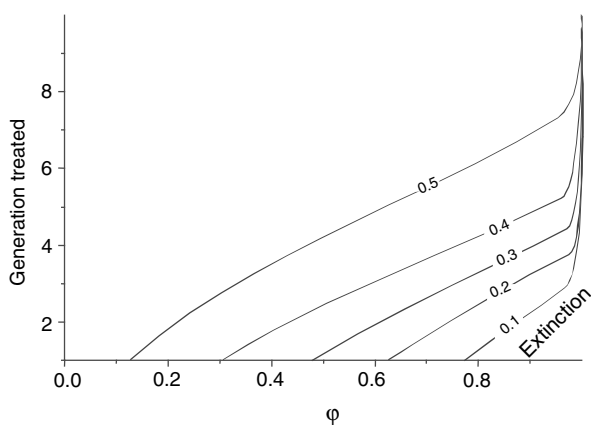


Figure 3 Establishment probabilities 20 generations after inoculation estimated from 10 000 simulations of eqn 4 under varying levels of eradication kill rates, ϕ , and times (generations post-inoculation) of eradication treatment, T ($x_0 = 5$, $C = 5$, $\gamma/K = 0.1$, $\sigma = 1.0$).

for most values of eradication timing and strength, the establishment rate did not vary substantially from the baseline (no treatment) value of 0.5. Establishment probabilities $< 10\%$ could only be achieved by applying a very high kill rate (e.g. > 0.9) within a very short time (e.g. 3 years) after inoculation.

A CASE STUDY: INVADING GYPSY MOTH POPULATIONS IN WESTERN NORTH AMERICA

We applied our modelling framework to historical data on isolated gypsy moth, *L. dispar*, populations in order to explore eradication strategies for this species. This insect species is native to most of the temperate forests of Eurasia but was accidentally introduced to eastern North America in 1869. It has gradually expanded its range, which now includes most of the northeastern USA and southeastern Canada (Liebhold *et al.* 1992). As the gypsy moth is a polyphagous foliage-feeding species, most regions of North America can ultimately be expected to support populations. In addition to the gradual unaided expansion of this insect's range, life stages are often inadvertently transported by humans to other portions of North America where they may be capable of founding isolated colonies (Sharov & Liebhold 1998). Therefore, government programmes are in place in most currently uninfested regions to detect new colonies using traps baited with a synthetic sex pheromone. These traps are very effective in detecting new colonies. When trap captures are positive at a location for two or more years, an attempt is usually made to confirm the presence of a population by searching out other life stages and then a treatment of the infested areas is applied to eradicate the population. These eradication programmes have been quite successful in preventing the expansion of gypsy moth into western North America (Dreistadt & Dahlsten 1989; Liebhold & McManus 1999).

Every year, the Washington State Department of Agriculture deploys several hundred pheromone traps in order to detect new gypsy moth colonies. We analysed records of the total numbers of males caught at each location from 1974 to 1996. Counts from several traps located in the same general area (because $> 95\%$ of trap counts in any year were zero, counts from contiguous populations could be easily identified) were combined to form a sum for each location in each year. These counts do not represent an estimate of population density but are simply measures of abundance (Sharov *et al.* 1995); they were used here as a proxy for colony population size. There was considerable undocumented variability in sampling intensity (numbers of traps) among years and among locations; however, these data still provide a general representation of the dynamics of isolated colonies. In all, 194 isolated colonies were detected from 1974 to 1996

(Fig. 4a). Of these 194 colonies detected, eradication treatments were applied against 32. Multiple treatments (two or more consecutive years of treatments) were required to eradicate nine of the 32 colonies and most treatments consisted of aerial application of the microbial pesticide, *Bacillus thuringiensis* (Liebhold & McManus 1999). Of the 162 colonies that went extinct without treatment, the majority (123) did so 1 year after they were first detected (Fig. 4a).

Colony survival probabilities as a function of time (Fig. 4b) fit an exponential model, $p(t) = e^{-1.659t}$, where $p(t)$ is the probability of surviving until year t (fit using nonlinear regression, multivariate secant method estimation). Extinction models also assume an exponential distribution for survival time $p(t) = e^{-\lambda t}$, where λ is the per year extinction rate (Foley 1994). For our data, $\lambda = 1.659 (\pm 0.0105)$, and the associated time to extinction for an average colony was $T_e = 1/\lambda = 0.603$ years. The observation that $T_e < 1$ is in agreement with our observation that most colonies went extinct in 1 year.

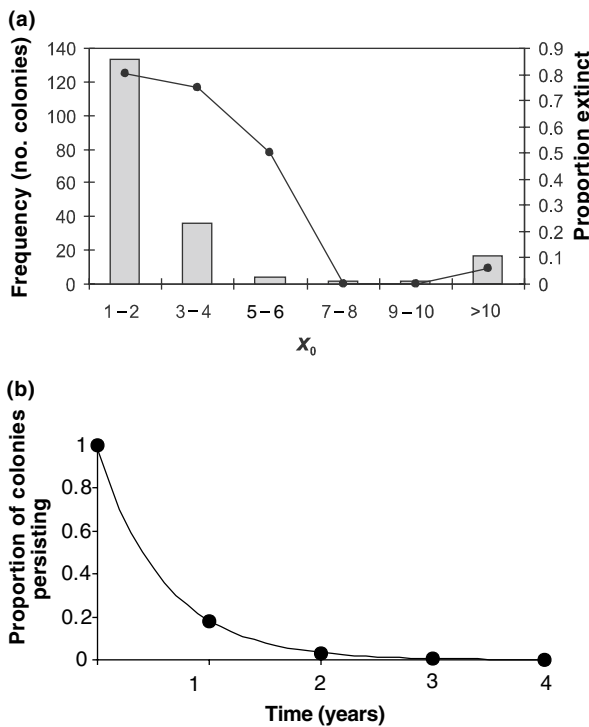


Figure 4 (a) Frequency distribution histogram of initial population size (x_0 = number of males trapped/colony) of historical gypsy moth colonies and proportion (line) of colonies that went extinct in their first year. (b) Probability of population persistence through time (colonies where eradication treatments were applied were not included) fit to the exponential model, $p(t) = e^{-1.659t}$ (d.f. = 4; $F = 224,193$; prob. of a greater $F = 0.0001$). Each dot represents the proportion of the 162 populations that persisted for each time interval.

The fact that extinction of gypsy moth colonies was more common at low vs. high initial population levels (Fig. 4a) suggests that stochasticity and/or Allee dynamics play an important role in the dynamics of these populations. Therefore, we used linear regression to fit the model of $\ln r_t$ as a function of x_t (eqn 3). A total of 225 observations were used to fit the model [successive years for each colony were used as independent observations (Fig. 1b); data were excluded if an eradication treatment was applied in a given year]. We estimated the intercept, $-C\gamma/K = -1.740$ (SE = 0.122) and the slope, $\gamma/K = 0.0163$ (SE = 0.00618). We assumed that sampling error was negligible and estimated σ as the SD of the residuals from this model (Higgins *et al.* 1997; SD = 1.774). Given these values we estimated the Allee extinction threshold as the negative intercept divided by the slope, $C = 1.740/0.0163 = 106.7$ males trapped per colony. Thus, on average, when fewer than 106.7 moths are detected in a colony, we can expect that most colonies will go extinct with no intervention. However, the stochastic influence was very high. We can see from Fig. 2 that a value of $\sigma = 1.774$ transforms the Allee extinction threshold into a highly continuous function. Therefore, even when $x_t < 106.7$ there is still a possibility of gypsy moth establishment.

We used simulations with the parameterized model to estimate the kill rates that would be required to eradicate isolated populations of varying sizes. Figure 5 shows the probability of gypsy moth establishment simulated using varying pre-treatment densities, x_0 , and eradication mortality rates, ϕ , and values of $-C\gamma/K$ and γ/K estimated from the historical gypsy moth data. When no eradication is applied

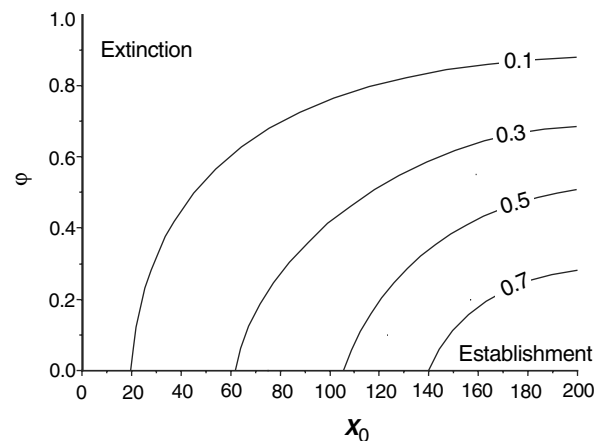


Figure 5 Simulated probabilities of gypsy moth establishment (20 years post-initiation) following eradication given a range of pre-treatment population levels (x_0) and eradication efficacies (ϕ). Eradication treatments are applied to the initial population ($T = 1$). Simulations were performed using parameter values fit to historical data (Fig. 1b).

($\phi = 0$), 50% establishment occurs when $x_0 = C = 106.7$. Of course, when the inoculum $x_0 > C$, establishment probability increases towards 100% and when $x_0 < C$, establishment decreases towards zero. Application of an eradication treatment decreased establishment probability for all values considered here, but the effect was most dramatic when the kill rate, ϕ , exceeded 0.5. Thus, any treatment causing $< 50\%$ mortality is unlikely to contribute towards eradication of low-density populations. In contrast, when a treatment that causes $> 80\%$ mortality is applied, there is a very high probability of successful eradication at all the population levels evaluated here.

DISCUSSION

Extinction of low-density populations can occur either as a result of stochasticity or Allee dynamics (Dennis 1989; Hopper & Roush 1993; Lande 1998). Both processes may contribute to the existence of a threshold, below which extinction is likely to occur. The demographic extinction threshold caused by an Allee effect and parametric thresholds (e.g. critical extinction rate/colonization rate, critical fraction of hosts vaccinated, or habitat loss thresholds) have been widely explored as part of efforts to devise more effective approaches to prevent species extinctions and in efforts to eradicate pathogens (Lande 1987; Anderson & May 1991; Bascombe & Rodriguez-Trelles 1998). However, there has been little investigation of the role of extinction thresholds in the design of efforts to eradicate alien animal and plant species.

The model that we use here is probably broadly applicable because virtually all species are affected by stochasticity and many may exhibit some form of Allee dynamics. The Allee effect has been documented in many different animal and plant species but the magnitude of this effect varies considerably depending on life-history characteristics (Berger 1990; Courchamp *et al.* 1999). The gypsy moth data analysed here indicate the existence of an Allee effect. The most likely explanation for Allee dynamics in this species is failure to find mates at low densities. Sharov *et al.* (1995) measured mating success in invading gypsy moth populations by deploying virgin females and then dissecting them to determine the presence of spermathecae. They replicated these observations over a range of abundance. Mating success was directly related to trap capture and 50% mating success corresponded to about five males per trap. As the measurement units of this threshold (moths/trap) are different from the Allee threshold we computed here (106.7 trapped moths/colony), it is impossible to make a direct comparison. However, a typical colony might be sampled by many pheromone traps, so that they appear to be in general agreement.

As life-history characteristics vary among different alien species, they will affect the extent to which the dynamics of

low-density populations are dominated by stochasticity and Allee effects. However, there are at least three important conclusions from this study that can be generalized for the selection of eradication strategies for all alien species. First, it is important to recognize that eradication may be achieved by killing or removing of $< 100\%$ of the population. Many previous reports state that eradication can only be achieved via 100% mortality of the population (DeBach 1964; Knipling 1966; Dahlsten *et al.* 1989) but this is clearly not the case. The work presented here indicates that eradication is likely to occur after killing only a fraction of the population. We believe that this is a more realistic objective for eradication treatments because 100% mortality would be very difficult to achieve in most settings.

Secondly, it is important to recognize that extinction will always be a stochastic process and for that reason eradication should always be considered in a probabilistic framework. When eradication treatments are planned, they should be designed to increase the probability of extinction, but extinction cannot be predicted with absolute certainty (unless 100% control is achieved!).

Thirdly, simulations (Fig. 3) demonstrated that the timing of an eradication treatment is likely to be as critical to the success of an eradication programme as is the level of mortality achieved. When populations grow sufficiently large, eradication becomes decreasingly feasible and other approaches to management must be considered (Sharov & Liebhold 1998). The ability to find colonies when they are still small enough to be successfully eradicated, depends upon the use of a sensitive system for detecting new populations. Methods for identifying the optimal balance of resources between detection and eradication are topics beyond the scope of this paper but should be pursued in the future.

Our simulations conducted using data for the gypsy moth illustrate how demographic data can be used to plan eradication strategies. For this organism, we can expect that when isolated populations are very low (indicated by < 20 trapped moths), eradication may not be necessary; populations are likely to go extinct with no intervention (Fig. 5). Populations of moderate abundance (indicated by 20–150 moths) can usually be eradicated following a single treatment that causes 80% mortality (Fig. 5). However, when populations are much higher (e.g. > 200 males), eradication may only be achieved via application of multiple treatments either in the same or successive generations. When populations are very high (e.g. > 1000 males), eradication may be very difficult to achieve via any practical methods. There is a long history of gypsy moth eradication treatments (Appelt 1985; Dreistadt & Dahlsten 1989); however, it has never been practical to test different eradication strategies experimentally. Application of microbial pesticides or mating disruption can be expected to reduce low-density gypsy moth populations by 75–95% (Sharov *et al.* 2002). The guidelines that we outlined

above generally agree with the historical success in applying these treatments to operational gypsy moth eradication programmes. One important caveat to these guidelines is that the model used here was fit to data from a specific region of North America; the numerical relationship of eradication success with population numbers and treatment mortality may vary in other habitats.

Any strategy to eradicate an alien species should consider the extent to which the life history of the species contributes to an Allee effect. Virtually every animal or plant species that requires sexual recombination for reproduction may be expected to exhibit some form of an Allee effect (Courchamp *et al.* 1999; Berec *et al.* 2001). The example organism illustrated here, the gypsy moth, is thus probably not particularly unique in the existence or strength of an Allee effect and some organisms could be expected to exhibit even stronger Allee dynamics. Of course there are some species (e.g. plant species that are capable of asexual reproduction) which may exhibit little or no Allee effect. Eradication of this type of organism may require an eradication treatment that removes a very high proportion of individuals but successful eradication can still be expected following <100% of all individuals solely due to the contribution of stochasticity to extinction (Fig. 2).

While the analysis presented here represents a generalized approach to devising eradication strategies, its primary shortcoming is the neglect of spatial relationships in modelling invasion dynamics. Both stochasticity and Allee dynamics play an important role in the expansion of invading populations (Lewis & Kareiva 1993; Keitt *et al.* 2001; South & Kenward 2001) and this is something that should be included in future work on detection and eradication strategies.

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