

Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations

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Summary

1. Understanding why invading populations sometimes fail to establish is of considerable relevance to the development of strategies for managing biological invasions.
2. Newly arriving populations tend to be sparse and are often influenced by Allee effects. Mating failure is a typical cause of Allee effects in low-density insect populations, and dispersion of individuals in space and time can exacerbate mate-location failure in invading populations.
3. Here we evaluate the relative importance of dispersal and sexual asynchrony as contributors to Allee effects in invading populations by adopting as a case study the gypsy moth (*Lymantria dispar* L.), an important insect defoliator for which considerable demographic information is available.
4. We used release–recapture experiments to parameterize a model that describes probabilities that males locate females along various spatial and temporal offsets between male and female adult emergence.
5. Based on these experimental results, we developed a generalized model of mating success that demonstrates the existence of an Allee threshold, below which introduced gypsy moth populations are likely to go extinct without any management intervention.

Key-words: expanding populations, isolated colonies, *Lymantria dispar*, protandry, stochastic diffusion model

Introduction

As a result of ever-increasing levels of world trade and travel, increasing numbers of non-indigenous species are being imported into new habitats (Levine & D'Antonio 2003; McCullough *et al.* 2006). Fortunately, most of these populations fail to establish (Williamson & Fitter 1996; Simberloff & Gibbons 2004), even when they arrive in favourable habitats in favourable seasons (Williamson 2006). Two primary demographic processes are responsible for the extinction of most low-density invading populations: Allee effects and stochasticity (Drake 2004; Taylor & Hastings 2005). The Allee effect refers to a decrease in the per capita population growth rate with decreasing density, and has been recognized as a

common cause of extinction in low-density populations (Allee *et al.* 1949; Stephens & Sutherland 1999; Taylor & Hastings 2005). Given the importance of Allee effects for the persistence of low-density populations, knowledge of this effect is essential to the development of strategies for managing invasive pests (Liebhold & Bascompte 2003), the establishment of species introduced for biological control (Fagan *et al.* 2002), and the conservation of endangered species (Stephens & Sutherland 1999).

Several mechanisms are known to be capable of producing an Allee effect. These include inbreeding depression, cooperative feeding, predator satiation and density-related mate-location failure (Courchamp, Clutton-Brock & Grenfell 1999; Stephens & Sutherland 1999). Populations may also be affected by Allee effects originating from several different mechanisms, and these multiple Allee effects may interact in unexpected ways to influence population dynamics (Berec, Angulo & Courchamp 2007).

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The inability of mates to locate each other at low densities is a common cause of Allee effects in sexually reproducing species (Dennis 1989; Berec, Boukal & Berec 2001). When invading populations arrive in a new area, dispersal away from the point of introduction prior to mating may exacerbate mate-location difficulties and, due to the low number of individuals, the search for mates may be more difficult than in their native range. Deterministic models demonstrate that random premating dispersal strengthens Allee effects due to mating failure, but increased mating efficiency (probability of mate location over a given distance) weakens Allee effects (Hopper & Roush 1993). Individual-based models have also been used to explore the interactions among dispersal, survival and mate-finding in relation to Allee effects (Berec *et al.* 2001; South & Kenward 2001).

Most studies of mate-location failure and its population-level effects have considered only the spatial distribution of individuals, yet temporal distributions are equally important (Calabrese & Fagan 2004; Robinet, Liebhold & Gray 2007). Reproductive life stages may be isolated in space as a result of their dispersal, but they may also be isolated in time due to within-population variability in the timing of sexual maturation and differences in the timing of sexual maturation between males and females (protandry).

In this paper, we investigate the combined effects of both spatial and temporal dispersion on mating success and subsequent Allee effects. We approach this problem using invading populations of the gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae) as a model system. This species is native to most of temperate Eurasia, and is currently invading North America. Allee effects are known to affect its establishment (Liebhold & Bascompte 2003; Whitmire & Tobin 2006) and spread (Johnson *et al.* 2006; Tobin *et al.* 2007). We extend the work of Robinet *et al.* (2007), which focused on the effects of temporal asynchrony in adult emergence on mating success, to include spatial effects. We accomplished this through a stochastic, individual-based and spatially explicit model that combines the effects of temporal and spatial dispersion of gypsy moth individuals on mating success. The model was based on a mark–recapture experiment that quantified mate-finding probabilities given varying temporal and spatial offsets between male and female emergence. We apply the model to predict mating success in hypothetical invading populations of various sizes, and, based on simulated numbers in the subsequent generation, we quantify the strength of the Allee effect caused by mating failure in this system to show that individual temporal and spatial distributions are both fundamental factors affecting population persistence.

Materials and methods

MEASUREMENT OF MATE-FINDING OVER TIME AND SPACE FROM RELEASE–RECAPTURE EXPERIMENTS

We conducted mark–recapture experiments to measure the probability that a male finds a female emerging at a given distance from the point of male emergence, and on a given day following male

emergence. In North American gypsy moth populations, females are flightless and emit a pheromone that attracts flying males for mating (Odell & Mastro 1980). In these experiments, we used a standard gypsy moth pheromone-baited trap (Sharov, Liebhold & Ravlin 1995) as a surrogate for a female, and used the recapture of released males as a surrogate for successful mate location.

Experiments were conducted during July–September 2003 and August 2004 in forested regions of Otis Air National Guard Base in Falmouth, Massachusetts. Timing of the experiments was designed to avoid coinciding with the period of adult emergence in background populations. In each replicate experiment, virgin laboratory-reared males with fully expanded wings were released within 9 h after their emergence. Separate releases of males ($n = 5–20$) were made simultaneously at points located in four cardinal directions (north-east, north-west, south-east and south-west) from the plot centre and at various distances (12.5, 25, 50, 100 and 150 m). Antennae of males released at a common distance were marked with an identically coloured fluorescent powder. A standard gypsy moth milk-carton trap baited with (+) disparture and containing a dimethyl dichloro-vinyl phosphate (DDVP) killing agent was located at plot centres. In approximately one-third of replicates, traps were installed on the same day as males were released (day 1), while approximately one-third were deployed the day after (day 2) and the remaining replicates after 2 days (day 3).

Three days after the release (by this time all released males were presumably either dead or had flown out of the plot), we recorded the cumulative recapture. This value was estimated as mean trap capture (for each combination of day of deployment and distance) as a fraction of the total number of males released. For individual combinations of time lag (days 1, 2 and 3) and distance from release point to trap, numbers of replicates (plots including that combination) varied from 1 to 22 (Table 1). We estimated the daily probability of attraction, p_i , as the proportion of released males captured per trap on each day, from $i = 1–3$, and for each of the five distances between release and recapture. The daily probability of attraction represents the fraction of males that did not die or become 'lost' (i.e. surviving males that fail to locate females), and successfully reached the pheromone-baited trap each day following release. Thus we estimated p_1 as the difference between the cumulative recapture from traps placed on days 2 and 1. Similarly, p_2 was estimated as the difference between day 2 and day 3 cumulative recaptures. To calculate p_3 , we assumed that the number of captures on day 4 (or after) was negligible, and it was estimated simply as the cumulative day 3 recapture.

For each time lag ($i = 1, 2$ or 3 days), we fitted a model of the daily probability of attraction (p_i) as a function of distance (x) between the point of release and the pheromone-baited trap using a negative exponential model:

$$p_i(x) = a_i \exp(-b_i x) \quad \text{eqn 1}$$

where a_i and b_i are fitted parameters. We used the optimization routine *nls(stats)* to fit this model to the data (R Development Core Team 2006). This probability p_i is the probability that a male emerging on day d is caught in a trap on day d if $i = 1$ (e.g. the trap was installed on the same day as the male releases); on day $d + 1$ if $i = 2$; or on day $d + 2$ if $i = 3$. Hereafter, we consider that the point of release is the point where the male emerged, and the location of the pheromone-baited trap is the point where the female emerged and called males via pheromones. We assumed that attractiveness of a pheromone-baited trap was equivalent to that of a virgin female due to the lack of definitive information to the contrary. There are reports that racemic (\pm) disparture baits are more attractive than a virgin female (Beroza *et al.* 1971; Stevens & Beroza 1972; Boness,

Table 1. Daily attraction probabilities (expressed as percentages) estimated from field experiments (males were released at various distances and various days before the placement of the pheromone-baited trap)

Distance (m)	Day 1				Day 2				Day 3			
	<i>n</i>	Cumul. obs.*	Daily obs.†	Daily mod.‡	<i>n</i>	Cumul. obs.	Daily obs.	Daily mod.	<i>n</i>	Cumul. obs.	Daily obs.	Daily mod.
12.5	4	29.1 (15.4)	9.1	11.0	1	20.0 (0)	14.4	16.8	1	5.6 (0)	5.6	4.7
25	4	33.6 (23.7)	11.1	9.7	1	22.5 (0)	19.7	14.5	1	2.8 (0)	2.8	4.3
	15		14.9	9.7	15		6.7	14.5	15		0.4	4.3
50	22	20.6 (14.1)	8.9	7.5	7	11.7 (7.0)	7.6	10.9	7	4.1 (2.3)	4.1	3.5
100	12	12.9 (5.4)	5.2	4.4	6	7.7 (3.1)	4.9	6.1	6	2.7 (1.9)	2.7	2.4
	15		2.8	4.4	15		7.6	6.1	15		0.9	2.4
150	18	7.0 (5.2)	0.3	2.6	6	6.7 (5.0)	5.5	3.4	6	1.2 (1.6)	1.2	1.6

*Cumulative recapture (SD in parentheses) from release–recapture experiments in Massachusetts (2003, 2004).

†Daily attraction probabilities, either derived from observed cumulative recapture or directly estimated (bold) from a separate field study (Virginia 2006).

‡Daily attraction probabilities modelled using equation 1. Model was not fitted from the separate field study (Virginia 2006) (bold) used to validate the model.

n, Number of replicate plots.

Eiter & Disselkotter 1977); but other reports that racemic disparlure is less attractive (Webb 1982). Additional studies indicated that (+) disparlure baits (similar to the pheromone lures used here) were slightly more attractive than females (Victor Mastro, unpublished data). As a result, the most parsimonious approach would be simply to assume that baits and females are equally attractive. Making this assumption is conservative, because if baits are more attractive than Allee effects would actually be stronger than our estimates indicate, and the main conclusion of this study would remain the same.

To validate the attraction model, we used data from a second field experiment conducted during summer 2006 in Farmville, VA, USA. This experiment had a similar design, except that males ($n = 56$ – 100) were released in separate sets of replicates at either 25 or 100 m from the pheromone-baited trap located at plot centres. Each time lag of trap placement was replicated with 15 plots (Table 1). Also, daily probability of attraction was measured directly from daily trap counts made on days 1, 2 and 3, rather than being based on the difference of cumulative recaptures. In this experiment, we also deployed traps at 3 and 4 days after male release (days 4 and 5) to verify that only a negligible number of males were recaptured after day 3.

DEMOGRAPHIC SIMULATION

The model of mate-finding described above was incorporated into a spatially explicit individual-based lattice model of gypsy moth dispersal, survival and mating over a single generation. The R Code (R Development Core Team 2006) for this model is provided in Appendix S1 in Supplementary material. This model represented a situation in which N egg masses were introduced at a single point in a region currently devoid of the species. We assumed that N egg masses were initially introduced in the middle of a 50×50 grid ($\Delta x = \Delta y = 0.01$ km). Each egg mass was composed of a fixed number of eggs (n_{egg}) with a 1 : 1 sex ratio. We coupled the following successive processes (tracking the fate and location of each individual) to estimate the mean number of fertilized egg masses in the following generation.

Dispersion in space

After eggs hatch, ballooning gypsy moth first instars disperse from their site of egg hatch (Mason & McManus 1981). We modelled

first-instar dispersal with a diffusion model in two spatial dimensions (x and y) at time t :

$$\frac{\partial U}{\partial t}(x,y,t) = D \left(\frac{\partial^2 U}{\partial x^2}(x,y,t) + \frac{\partial^2 U}{\partial y^2}(x,y,t) \right), \quad \text{eqn 2}$$

where D is the diffusion coefficient ($D = 0.003$ km² per generation; Shigesada & Kawasaki 1997; Liebhold & Tobin 2006) and U is the standardized population density satisfying:

$$\iint U(x,y,t) dx dy = 1 \quad \forall t \geq 0, \quad \text{eqn 3}$$

or, more precisely, the quantity $U(x,y,t)$ is the probability that a larva resides at location (x,y) at time t . We solved equation 2 on the time interval $[0,1]$ (time for one generation). Then each individual (males and females) was allocated to the cell to which it dispersed according to this probability distribution.

Mortality

Gypsy moths are affected by a multitude of mortality factors during their life span (predators, parasitoids and pathogens; Elkinton & Liebhold 1990). Although this mortality may be density-dependent, modelling this relationship fell beyond the scope of this study. Therefore we applied a fixed (but approximately realistic) constant mortality rate of 95% from egg hatch to adult emergence (Campbell 1967; Elkinton & Liebhold 1990), then randomly chose surviving individuals. We refer to the survival rate parameter, $surv = 0.05$.

With regard to adult survival, the mate-finding model (equation 1) implicitly accounted for male survival because over the time lag, i , between release and recapture the model accounts for both male mortality and for males becoming lost in space. In the full demographic model, we assumed for simplification that females lived only a single day. This assumption is justified because: (a) previous models indicate that female longevity has a small effect on mating success (Robinet *et al.* 2007); (b) field studies indicate that daily rates of predation on females are high, exceeding 50% (Sharov *et al.* 1995); and (c) even though females are able to call for up to 3 days under laboratory conditions, their ability to mate and produce viable offspring declines dramatically after 1 day (Doane 1976; Richerson, Cameron & Brown 1976).

Table 2. Parameters used in the model, range values and (in parentheses) particular values considered along this study

Parameter	Description	Values
N	Number of egg masses initially introduced	1–10 by 1 (5)
n_{egg}	Number of eggs hatching from a single egg mass	200–500 by 100 (300)
D	Diffusion coefficient related to larval dispersal: dispersion in space	0.001–0.01 by 0.0005 (0.003) km ² per generation
surv	Survival rate from egg hatch to adult emergence	0.05
SD	SD of Gaussian function: dispersion in maturation time	5 or 10 days
ΔT	Protandry (difference between male and female mean maturation time): dispersion in maturation time	0–15 days by 1 (5)
em_d (ef_d)	Daily rate of male (female) sexual maturation	Simulated
m	Probability that a male mates a female following successful attraction	0.91

Dispersion in time

Gypsy moth sexual maturation (moth emergence) occurs in mid-summer, but the dates vary with climatic conditions (Régnière & Sharov 1998; Robinet *et al.* 2007). Adult emergence typically spans a period of 2–3 weeks, with peak male emergence usually occurring a few days before the female peak. This time lag, protandry, has been widely recognized to be an adaptive trait in widely established populations, but recent studies show that in low-density populations, protandry can enhance Allee effects and lead to extinction (Calabrese & Fagan 2004; Robinet *et al.* 2007). Robinet *et al.* (2007) used a detailed temperature-based phenological model specific for the gypsy moth (Gray 2004) to generate the temporal distribution of gypsy moth adult emergence for each sex from historical daily minimum and maximum temperatures. The model predicted considerable geographical variation in protandry, ranging from 3 to 6 days.

Additionally, Robinet *et al.* (2007) showed that a Gaussian distribution performed well in representing actual emergence curves based on physiological time. Therefore we adopted this approach to explore the effects of temporal asynchrony on mating success. We used Gaussian functions (\bar{x} = 100 days for males, an arbitrary value that fixes the date of the male emergence peak while avoiding negative dates) with two SD values (5 and 10 days) to simulate emergence time distributions, and we also considered various delays (protandry) between mean male and female emergence times (ΔT = 0–10 days). The standard deviation represented the temporal dispersion of the emergence: for example, if the standard deviation was low, adults emerged over a short period. Based on the probability that adults emerge on day d (em_d for males; ef_d for females), we randomly chose the emergence day for each individual.

Mating success

Once adults have emerged, mating success depends on the distance between males and females. The experimentally derived probability-of-attraction model (equation 1) provided the probability that a male that emerged at a given distance from a female succeeded in finding her at a given time after his emergence. Then we multiplied this probability by the probability that, once the male has come into proximity to a female, he actually mates: m = 0.91 (Charlton & Cardé 1990). We considered that males could engage in multiple matings and mate with one female independently from the others, but multiple matings were not simulated explicitly. More precisely, we did not account for the distance a male had to fly to mate from one female to another (we always considered the distance between male emergence location and each calling female location). In fact,

we did not actually determine which male could mate each female: we calculated the probability that a female is mated at least by one male (given the spatial and temporal coordinates of the surrounding males), then randomly selected whether she was mated or not based on this probability. Finally, we summed the simulated number of mated females, and assumed that this was identical to the number of new egg masses in the following generation (gypsy moth females are capable of laying only a single egg mass). Hence, if the final number of mated females was above N (the number of egg masses introduced initially), we concluded that the population growth rate was greater than unity and that the population could persist.

To estimate the Allee effect and find the critical number of egg masses needed for the population to persist (N_c), we considered a realistic level of temporal asynchrony (ΔT = 5, SD = 10) (Robinet *et al.* 2007), and conducted 200 simulations for various numbers of initially colonizing egg masses (N = 1–10 by 1), assuming n_{egg} = 200–500 by 100 and D = 0.003 km² per generation.

We also conducted simulations with varying levels of protandry (ΔT = 0–15 by 1, in which 0 = synchronous male and female emergence) and larval dispersal (D = 0.001–0.01 by 0.0005; cf. equation 2). For each parameter combination, we generated 500 replicate simulations; five egg masses were initially introduced, n_{egg} = 300; and we considered SD = 5 or SD = 10. The list of parameters used in this study is given in Table 2.

Results

MEASUREMENT OF MATE-FINDING OVER TIME AND SPACE FROM RELEASE–RECAPTURE EXPERIMENTS

A total of 5967 adult males were released and 684 (11.5%) were recaptured. Highest cumulative recapture occurred when pheromone-baited traps were installed on the same day as males were released, and recapture decreased with increasing temporal lags between male release and trap deployment (Table 1). Cumulative recapture also tended to decrease with increasing distance between points of release and trap location. Although recaptures were marginally higher at 25 than at 12.5 m, this difference was not significant for day 1 (two-sample t -test = -0.31 , df = 5.14, P = 0.77) and comparable for day 2 (no replicates for both distances, but 20% of males were recaptured at 12.5 m and 22.5% at 25 m). We estimated daily attraction probabilities (Table 1) based on the cumulative recapture, and found that attraction probability was greatest (19.7%) on day 2 at 25 m (Table 1).

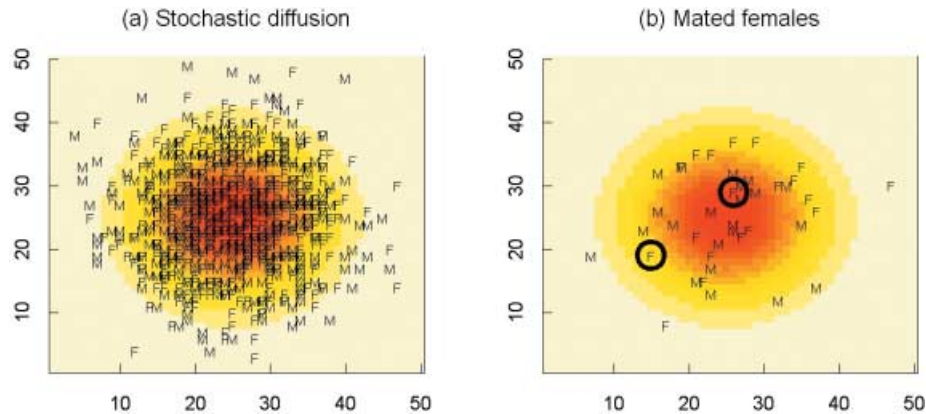


Fig. 1. Example simulation of successive stochastic processes ($\Delta T = 5$, $SD = 10$, $n_{\text{egg}} = 300$, $N = 3$): (a) postdispersal numbers of males (M) and females (F); (b) the spatial distribution of surviving individuals; circles indicate which females were finally mated. Background shading represents the redistribution probabilities from the larval diffusion model (equation 2).

Table 3. Parameter estimates \pm SE, P values corresponding to a t -test and coefficients of determination for the three models of daily attraction probability (from equation 1) estimated from observations in Massachusetts (2003, 2004)

Day	Parameter	Estimate	P	R^2
1	a_1	0.126 (± 0.023)	0.012	0.83
	b_1	0.010 (± 0.004)	0.088	
2	a_2	0.195 (± 0.046)	0.024	0.71
	b_2	0.012 (± 0.006)	0.138	
3	a_3	0.052 (± 0.011)	0.017	0.66
	b_3	0.008 (± 0.004)	0.147	

Parameters of the attraction probability equation (equation 1) estimated from observed values are listed in Table 3. Parameters a_i were significant whereas b_i were not. Based on the coefficient of determination, the models explained 66–82% of the variation in attraction probabilities.

Comparison of model predictions with observations from the verification experiment (Virginia 2006) (bold text in Table 1) indicated an average absolute error of $< 4\%$. Moreover, a negligible number of males ($< 0.3\%$) were recaptured on days 4 and 5, verifying our assumption that by that time most males were dead or lost. Consequently, our model provides an adequate representation of daily attraction probabilities at various spatial and temporal lags between the release of males (roughly equivalent to male emergence) and recapture at a pheromone-baited trap (roughly equivalent to attraction to a newly emerged female).

DEMOGRAPHIC SIMULATION

We conducted simulations to predict the number of fertilized egg masses in year $t + 1$ following the introduction of a specific number of egg masses at a single point in year t , followed by larval dispersal, mortality, variability in dates of sexual maturation, and mate location success (Fig. 1). This model

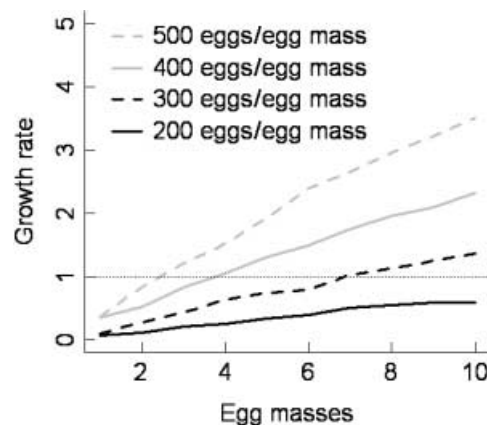


Fig. 2. Allee effect resulting from mating failure. For various numbers of eggs per egg mass ($n_{\text{egg}} = 200, 300, 400$ and 500), we generated 200 simulations for varying numbers of egg masses introduced ($N = 1-10$) and predicted the mean number of females mated over all replicate simulations ($\Delta T = 5$, $SD = 10$). The growth rate is defined by the number of females mated divided by the number of egg masses initially introduced.

indicated that the population growth rate was positively related to the initial number of egg masses introduced, N (Fig. 2). Not surprisingly, the slope of this relationship is strongly influenced by fecundity (eggs/egg mass). The graphs in Fig. 2 are typical of a strong Allee effect because growth rates fall below 1 (representing population replacement) at low densities (Taylor & Hastings 2005). When growth falls below 1, populations will decline toward extinction; thus the number of egg masses at which population growth equals 1 represents the Allee threshold, N_c , which is thus the minimum population size necessary for establishment: $N_c = 18$ egg masses for $n_{\text{egg}} = 200$ eggs (not shown in the figure); $N_c = 8$ egg masses for 300 eggs; $N_c = 4$ egg masses for 400 eggs; and $N_c = 3$ egg masses for 500 eggs (Fig. 2). Gypsy moth fecundity varies inversely with density (Campbell 1978), so it is quite likely that egg masses introduced from an outbreak area would yield a low number (e.g. 200–300) of viable eggs.

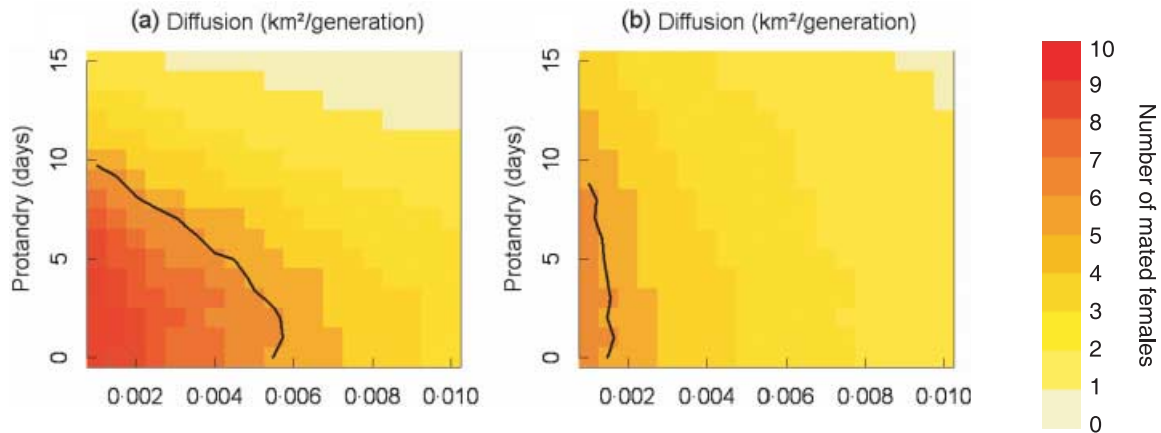


Fig. 3. Mating success as a function of temporal dispersion (ΔT , days) and spatial dispersion (D , km^2 per generation). We assumed that $N = 5$ egg masses were initially introduced; $n_{\text{egg}} = 300$ eggs per egg mass, and calculated the mean number of mated females over 500 iterations. We assumed (a) low dispersion in emergence time ($\text{SD} = 5$); (b) high dispersion ($\text{SD} = 10$). Black line, threshold of five mated females (corresponding to a growth rate of 1).

We fixed the number of egg masses initially introduced as $N = 5$ and the number of eggs per egg mass as $n_{\text{egg}} = 300$, and conducted simulations under varying levels of temporal and spatial dispersion of individuals to determine their effect on mating success (Fig. 3). When either temporal or spatial dispersion was high, males were more easily lost and mating success decreased. Protandry also had a strong effect on mating success and population growth. Together, protandry, variability in developmental times, and prereproductive dispersal combine to determine mating frequency and consequently the probability of population persistence. For example, a low level of variability in the timing of emergence (e.g. $\text{SD} = 5$ days), and a short delay between male and female emergence times (low protandry) allowed the population to persist, but establishment probability rapidly decreased with increased protandry (Fig. 3a). When variability in development time is much higher (e.g. $\text{SD} = 10$ days), dispersal strongly reduced mating success but the effect of protandry was diminished (Fig. 3b). In this case, mating success is globally low, thereby reducing the negative effect of larval dispersal as well as the protandry effect. In this situation, the weak effect of protandry probably arises because sexual maturation is so dispersed in time that the overlap of male and female reproductive periods is low, even in the case of low protandry. We also note that when temporal variability in maturation times is great, prereproductive dispersal would need to be short for the population to persist.

Discussion

The quantification of Allee effects in natural populations is often challenging due to the difficulties in sampling low-density populations (Courchamp *et al.* 1999). However, for species management, whether for population control or conservation, identifying the minimum number of individuals necessary for population persistence is fundamental (Stephens & Sutherland 1999; Taylor & Hastings 2005; Berec *et al.*

2007). This study provides an example of how demographic information can be combined to quantify Allee effects and estimate Allee thresholds in a model system (gypsy moth). This approach might ultimately be applied to other species that are difficult to sample at low densities, the management of which would benefit from a fundamental understanding of Allee dynamics.

Allee effects can arise from a variety of processes (Courchamp *et al.* 1999; Stephens & Sutherland 1999), although this study addressed only mate-location failure as a mechanism. In the case of the gypsy moth, mate-location failure has previously been demonstrated to be a cause of Allee effects (Sharov *et al.* 1995; Tcheslavskaja, Brewster & Sharov 2002), but low-density populations are also known to be strongly influenced by generalist predators operating through a type II functional response (Elkinton *et al.* 1996; Elkinton, Liebhold & Muzika 2004). This type of predation is well known to contribute to an Allee effect (Gascoigne & Lipcius 2004), and it is likely that predation and mate-location failure jointly contribute to Allee effects in this system (Stephens, Sutherland & Freckleton 1999; Berec *et al.* 2007). Thus the model presented here provides a conservative representation of the strength of Allee effects in low-density gypsy moth populations.

Our simulations here considered only the fate of a population over a single generation following the introduction of a given number of egg masses at a single location. While the value of the growth rate, the number of mated females divided by N , calculated for this first generation is a good indicator of the ultimate fate of the population, it is quite likely that growth rates might change in subsequent generations. Specifically, any egg masses that initialize the second generation are likely to be more widely dispersed over space, in contrast to egg masses in the first generation that are assumed to begin from an introduction at a single point. Such spatial dispersion in subsequent generations can be expected to result in decreased mating success, and ultimately enhanced the Allee effects and increased probabilities of extinction. Simulations that follow

populations over several generations are needed in order to estimate extinction probabilities more precisely.

One distinctive aspect of the gypsy moth system is that the abundance of low-density populations may be measured relatively easily using pheromone-baited traps. As a consequence, it has been possible to use trap-catch data to quantify a strong Allee effect in low-density populations (Liebhold & Bascombe 2003; Johnson *et al.* 2006; Whitmire & Tobin 2006; Tobin *et al.* 2007). In each of these studies, population density was expressed in terms of male trap catch, so it is not possible to compare these empirically estimated Allee effects directly with the demographic models derived here, which express abundance in terms of total population size. Nevertheless, these studies are in general agreement with the strength of the Allee effect reported here.

Tobin *et al.* (2007) used gypsy moth trap-catch data from a large region of the eastern USA to document the existence of geographical and temporal variation in the strength of Allee effects. The cause of this variation is not completely clear. Robinet *et al.* (2007) demonstrated that regional variability in developmental rates caused by climatic variation results in a geographical gradient of mating success. Our study confirms the importance of the temporal distribution of emergence dates: mating success declines as individuals in the population emerge over longer periods, even if protandry is not strong and larval dispersal is also low. Considerable variability in the distribution of adult emergence dates has been observed in some climatic regions that are otherwise favourable for gypsy moth development (Robinet *et al.* 2007), and this could contribute to decreased probabilities of establishment. However, this geographical variation in the dispersion and synchronization of male and female maturation does not necessarily correspond with the geographical variation in the strength of Allee effects observed empirically (Tobin *et al.* 2007). It is possible that some of the other demographic parameters (e.g. fecundity) could also vary geographically, and this might also contribute to the empirically observed variation in the strength of Allee effects. Tobin *et al.* (2007) also speculated that the apparent variation in Allee effects could be the result of variability in the occurrence of mass dispersal of adult males from nearby high-density areas; this supplementation of male numbers via immigration could greatly diminish the strength of Allee effects (Tobin & Blackburn 2008).

Mate-location failure creates an Allee threshold; if founding populations fall below this threshold, extinction is likely and invasion is thus likely to fail. The demographic characteristics that we considered here for their influence on Allee dynamics were somewhat limited, but nevertheless provide some fundamental understanding of how demographic characteristics interact. While there has been some exploration of how temporal variability in developmental time and protandry promote Allee effects due to mate-location failure (Calabrese & Fagan 2004; Robinet *et al.* 2007), the effect of premating dispersal has received less attention. Ironically, dispersal is often considered a desirable trait for a successful invader (Baker 1986), but results reported here indicate that premating dispersal may be inversely related to probability of

establishment. Evidence that dispersal can intensify the probability of extinction of invading populations in the presence of Allee effects has been found previously (Hopper & Rousch 1993; Jonsen, Bouchier & Roland 2007). Of course, dispersal ability may be a critical trait facilitating spread, and the contrasting effects of dispersal on invasion success highlight the need to consider each stage of the invasion process separately when predicting invasion success (Williamson 2006). It also may be important to consider demographic details in such exercises, because some species, particularly those that reproduce parthenogenically, may not exhibit any Allee effect due to mate-location failure (Fauvergue *et al.* 2007).

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. R-code for the mating success model.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2008.1417.x>

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