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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 a question of considerable relevance to the development of strategies for managing biological invasions.

2. Newly arriving populations tend to be sparse and 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 furthermore exasperate 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, 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.

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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 and 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 favorable habitats in favorable 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 to the persistence of low-density populations, knowledge of this effect is essential to the development of strategies for managing invasive pests (Liebhold & Bascompte 2003), establishment of species introduced for biological control (Fagan *et al*. 2002) or 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).

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

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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 pre-mating 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 only considered 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 (i.e., 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 upon a mark-recapture experiment that quantified mate-finding probabilities given varying temporal and spatial offsets between male and female emergence.

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We apply the model to predict mating success in hypothetical invading populations of various sizes, and based upon 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.

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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 that emerges 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 not coincide 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 hours after their emergence. Separate releases of males (n = 5-20) were simultaneously made at points located in four cardinal directions (north-east, north-west, south-east and south-west) from the plot center 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 colored fluorescent powder. A standard gypsy moth milk carton trap baited with (+) disparlure and containing a DDVP killing agent was located at plot centers. In approximately ⅓ of replicates, traps were installed the same day males were released ("day 1"), while approximately ⅓ were deployed the day after ("day 2") and the remaining replicates were deployed after 2 days ("day 3").

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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 (day 1, 2, and 3) and distance from release point to trap, numbers of replicates (plots which included 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 $i = 1$ to 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 get 'lost' 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 day 2 and day 1. Similarly, p_2 was estimated as the difference between the day 2 and day 3 cumulative recaptures. For the calculation of 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.e., $i = 1$, 2, or 3 days), we fit a model of the daily probability of attraction (p_i) as a function of the distance (x) between the point of release and the pheromone-baited trap using a negative exponential model,

$$p_i(x) = a_i \exp(-b_i x) \ , \qquad \text{(Eq. 1)}$$

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 the same day than 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

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that of a virgin female due to the lack of definitive information to the contrary. There are both reports that racemic (+/-) disparlure baits are more attractive than a virgin female (Beroza *et al*. 1971; Stevens & Beroza 1972; Boness, Eiter & Disselnkotter 1977) and 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 to simply assume that baits and females are equally attractive. Making this assumption is conservative because if baits are more attractive then 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 the summer 2006 in Farmville, Virginia. 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 centers. Each time lag of trap placement was replicated with 15 plots (Table 1). Also, daily probability of attraction was directly measured from daily trap counts made on day 1, day 2, and day 3 rather than being based on the difference of cumulative recaptures. In this experiment, we also deployed traps 3 and 4 days after male release (day 4 and day 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

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Appendix S1. 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.

(1) Dispersion in space. After eggs hatch, ballooning gypsy moth first-instars disperse from their site of egg hatch (Mason & McManus 1981). We modeled first-instar dispersal with a diffusion model in two spatial dimensions (x and y) at time t,

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

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

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

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 they dispersed according to this probability distribution.

(2) Mortality. Gypsy moths are affected by a multitude of mortality factors during their life span (e.g., predators, parasitoids and pathogens) (Elkinton & Liebhold 1990). Though this mortality may be density-dependent, modeling 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), and

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then we 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 (i.e., surviving males that fail to locate females). In the full demographic model, we assumed for simplification that females only lived a single day. This assumption is justified because: a) previous models indicated that female longevity has a small effect on mating success (Robinet *et al*. 2007), b) field studies indicated that daily rates of predation on females is 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 dramatically declines after 1 day (Doane 1976; Richerson, Cameron & Brown 1976).

(3) 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 geographic variation in protandry, ranging from 3-6 days.

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Additionally, Robinet *et al*. (2007) showed that a Gaussian distribution performed well in representing actual emergence curves based upon 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 which fixes the date of the male emergence peak while avoiding negative dates) with two standard deviation values (*SD* = 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 to 10 days). The standard deviation represented the temporal dispersion of the emergence: e.g., 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 and ef_d for females), we randomly chose the emergence day for each individual.

(4) 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 to find her at a given time after his emergence. Then, we multiplied this probability by the probability that, once the male has come in 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 explicitly simulated. More precisely, we did not account for the distance a male had to fly to mate from one female to another one (we always considered the distance between the male emergence location and each calling female location). In fact, we did not actually determine which male can mate each female since we calculated the probability that a female is mated at least by one male (given the spatial and temporal coordinates of the surrounding males), and then we randomly selected whether she was mated or not based on

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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 initially introduced), 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 and SD = 10) (Robinet *et al*. 2007) and conducted 200 simulations for various numbers of initially colonizing egg masses (N = 1 to 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 to 15 by 1 in which 0 = synchronous male and female emergence) and larval dispersal (D = 0.001 to 0.01 by 0.0005; cf. equation 2). For each parameter combination, we generated 500 replicate simulations, 5 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.

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RESULTS

Measurement of mate-finding over time and space from release-recapture experiments

A total of 5,967 adult males were released and 684 (11.5%) were recaptured. Highest cumulative recapture occurred when pheromone-baited traps were installed the same day that 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 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 upon the cumulative recapture and found that attraction probability was greatest (19.7%) on day 2 at 25 m (Table 1).

Parameters of the attraction probability equation (Eq. 1) estimated from observed values are listed in Table 3. Parameters a_i were significant whereas b_i were not. Based upon 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 lines 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

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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 indicated that the population growth rate was positively related with the initial number 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_{egg} = 200 eggs (not shown in the figure); N_c = 8 egg-masses for n_{egg} = 300 eggs; N_c = 4 egg-masses for n_{egg} = 400 eggs; and N_c = 3 egg-masses for 500 eggs (Figure 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.

We fixed the number of egg-masses initially introduced as N = 5 and the number of eggs per egg-mass as n_{egg} = 300, and conducted simulations under varying levels of temporal and spatial dispersion of individuals to determine their effect on mating success (Figure 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

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population growth. Together, protandry, variability in developmental times, and pre-reproductive 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., *SD* = 5 days), and a short delay between male and female emergence times (low protandry) allows the population to persist, but establishment probability rapidly decreased with increased protandry (Fig. 3a). When variability in development time is much higher (e.g., *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, pre-reproductive dispersal would need to be short for the population to persist.

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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 which are difficult to sample at low densities, but whose management 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) though this study only addressed 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; Tcheslavskaia, 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 only considered 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

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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 would ultimately be needed in order to more precisely estimate extinction probabilities.

One rather unique 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 & Bascompte 2003; Whitmire & Tobin 2006; Johnson *et al*. 2006; Tobin *et al*. 2007). Because in each of these studies, population density was expressed in terms of male trap catch, it is not possible to directly compare these empirically estimated Allee effects with the demographic models derived here that 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

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observed in some climatic regions that are otherwise favorable 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 geographic variation in the strength of Allee effects empirically observed (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 and 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 they 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 pre-mating dispersal has received less attention. Ironically, dispersal is often considered a desirable trait for a successful invader (e.g., Baker 1986) but results reported here indicate that pre-mating dispersal may be inversely related with probability of establishment. Evidence that dispersal can intensify the probability of extinction of invading populations in the presence of Allee effects has previously been found (Hopper & Rousch 1993; Jonsen, Bourchier & Roland 2007). Of course, dispersal ability may be a critical trait facilitating spread, and the contrasting effects of dispersal on invasion success highlights the need to consider each stage of the invasion

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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 effect (Fauvergue *et al*. 2007).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

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

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TABLES

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). These data represent:

(1) cumulative recapture (column labeled "Cumul obs.") (standard deviation in parentheses), from release-recapture experiments in Massachusetts (2003, 2004);

(2) daily attraction probabilities (column labeled "Daily obs.") either derived from the observed cumulative recapture (1), or directly estimated (in bold) from a separate field study (Virginia, 2006);

(3) daily attraction probabilities (column labeled "Daily mod.") modeled using equation 1. Model was not fit from the separate field study (Virginia, 2006) (bold values), used to validate the model. Number of replicate plots is given by *n*.

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Distance (m)	DAY 1				DAY 2				DAY 3			
	n	Cumul. obs.	Daily obs.	Daily mod.	*n*	Cumul obs.	Daily obs.	Daily mod.	*n*	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 **15**	33.6 (23.7)	11.1 **14.9**	9.7 **9.7**	1 **15**	22.5 (0)	19.7 **6.7**	14.5 **14.5**	1 **15**	2.8 (0)	2.8 **0.4**	4.3 **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 **15**	12.9 (5.4)	5.2 **2.8**	4.4 **4.4**	6 **15**	7.7 (3.1)	4.9 **7.6**	6.1 **6.1**	6 **15**	2.7 (1.9)	2.7 **0.9**	2.4 **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

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Table 2. Parameters used in the model, their range values and, in bracket, some particular values considered along this study.

Parameters	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 the larval dispersal, *representing the dispersion in space*.	0.001-0.01 by 0.0005 (0.003) km²/generation
$surv$	Survival rate from egg hatch to adult emergence	0.05
SD	Standard deviation of the Gaussian function, *representing the dispersion in maturation time*.	5 or 10 days
ΔT	Protandry (difference between male and female mean maturation time), *representing 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

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

Day	Parameters	Estimates	*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	

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FIGURES

Figure 1. Example simulation of successive stochastic processes ($\Delta T = 5$, $SD = 10$, $n_{egg} = 300$, $N = 3$): (a) post-dispersal 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 (Eq. 2).

Figure 2. Allee effect resulting from mating failure. For various numbers of eggs per egg mass ($n_{egg} = 200$, 300, 400 and 500), we generated 200 simulations for varying numbers of egg masses introduced ($N = 1$ to 10) and we 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.

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

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Figure 1.

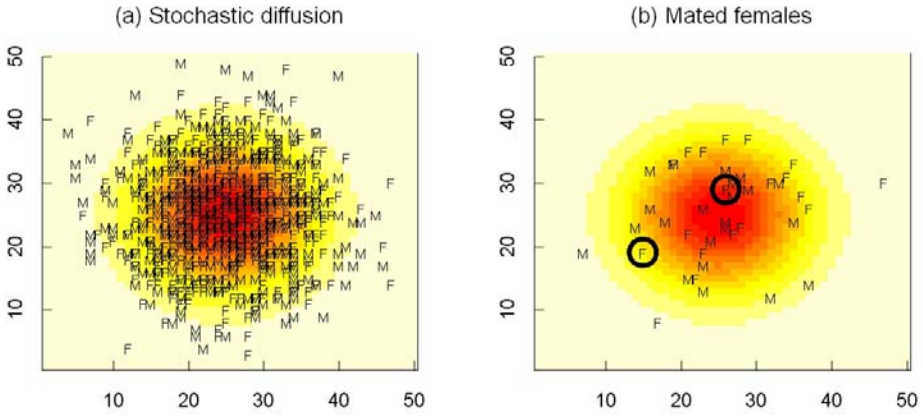

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Figure 2.

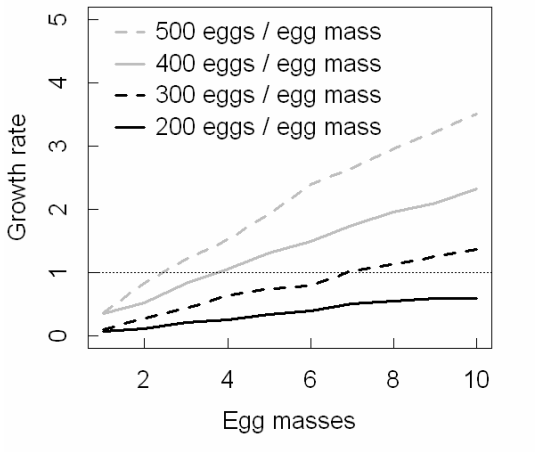

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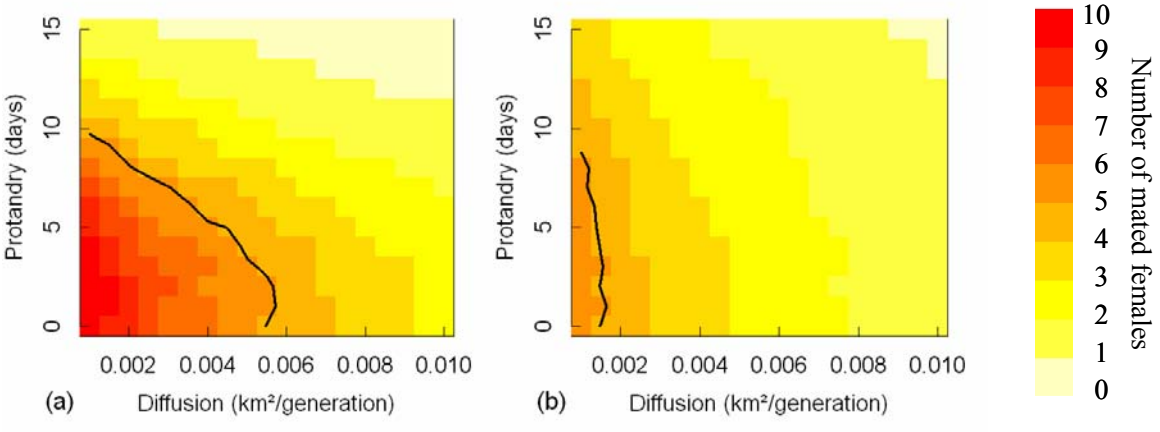
Figure 3.



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