Lost and lonely gypsy moths: mate location failure as a mechanism causing an Allee effect in the gypsy moth

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LOST AND LONELY GYPSY MOTHS: MATE LOCATION FAILURE AS A MECHANISM CAUSING AN ALLEE EFFECT IN THE GYPSY MOTH

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INTRODUCTION

Various process affecting low density populations may generate **Allee effects** and profoundly affect population persistence. Understanding these effects could improve conservation strategies and invasion control. While mate-finding is often mentioned in the literature as a cause of Allee dynamics, the underlying mechanisms are still unclear. **Mating failure** can result from both **spatial and temporal isolation of males and females**. Here we address both issues and more particularly the temporal issue since it has received little attention up to now.

Lost in time : temporal asynchrony

OBJECTIVES

To explore the effects of
1) dispersion of sexual maturation times, and
2) time-lag between male and female mean maturation (protandry)
on mating success.

METHODS

1) Generalized model: Distributions of ♂ and ♀ sexual maturation times were generated using Gaussian density functions with varying standard deviation and varying lags between the mean time of ♂ and ♀ maturation. Mating probability was derived from a negative exponential model (eq. 1) where P_d is the probability that a female is mated on day *d* given the number of mature males M_d on this day (depending on the daily rate of males becoming sexually mature, male longevity and the total number of males):

$$P_d = 1 - \exp(- s\, M_d) \qquad \text{(eq. 1)}$$

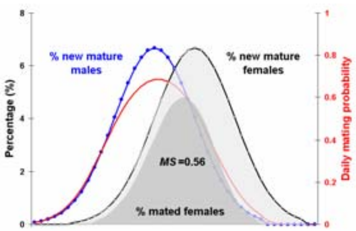

Figure 1: Role of male and female maturation times on daily mating probability and global mating success *MS*.

Population-level mating success *MS* was based upon these daily mating probabilities and the temporal distribution of females (calculated from the daily rate of female sexual maturation and female longevity) (Fig. 1).

2) Gypsy moth case study: emergence curves were estimated using a Life Stage (GLS) Model (Gray 2004) based upon daily temperature. For each day, we estimated the probability that each female was mated using a model derived from Sharov *et al*. (1995) (eq. 1 with *s*=0.15). Abundance of males was described by the season-long trap capture of males (*TC*) and it was set constant over space for simplification. Mating success was calculated using weather station data from 7,591 locations across North America from 1960 to 2000.

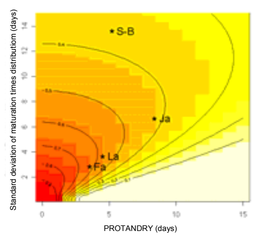

Figure 2: Effects of dispersion of maturation times and protandry (delay between males and females mean time maturation) on mating success *MS*.

RESULTS

1) Generalized model: both dispersion in developmental time and lags in male and female maturation affected mating success (Fig. 2). Females that matured late, or near the mean time, had a negligible mating probability (due to lack of males) whereas the females maturing earliest were the main contributors to population growth (Fig. 1).

2) Gypsy moth case study:

- Mating success is non uniformly distributed across North America (Fig. 3).
- Mating failure in extreme northern and southern areas is caused by low or no emergence of adults.
- A central zone where mating is most successful, but not yet occupied by the gypsy moth, stretches across the USA.
- Unfavorable areas due to different causes:
  The Rocky Mountain area is clearly unfavorable for mate-finding (long time lag between males and females: 8.4 days, and relatively short dispersion of emergence curves: *sd* = 6.7 days in Jackson, WY). Surprisingly, coastal California was also quite unfavorable with a reasonable time lag of 5.2 days but extremely high dispersion of emergence times: *sd* = 13.6 days (in Santa Barbara, CA) (*). This result demonstrates the complexity of the relationship between protandry and variability in development times, and mating success.

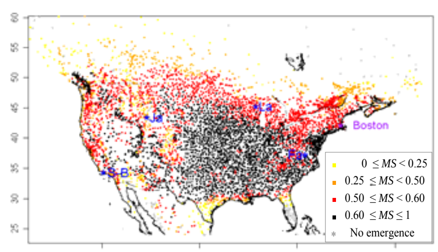

Figure 3: Average mating success of gypsy moth over 1960-2000, based on a single oviposition date (August 1), a season-long trap capture of 100 males, emergence curves predicted by the GLS phenology model and the mating model developed in this study.

(*) Indeed, relatively warm temperatures could increase the variability in timing of egg hatch. Even though this variability allows male and female reproductive periods to overlap, it causes a severe decrease in the daily density of mature males. Since the mating probability increases exponentially with the daily number of mature males (see eq. 1), a large span of the emergence curve is paradoxically unfavorable for mating success.

3) Comparison of both models: mating success values predicted by the generalized model are highly consistent with the values predicted by the more realistic gypsy moth-specific model (absolute errors ≤ 0.01), using the mean protandry and the mean variability in males development times. Thus it is not necessary to perform detailed simulations in order to estimate mating success with an acceptable level of accuracy; assuming a normal distribution of maturation times is correct.

Lost in space : stochastic diffusion

OBJECTIVES

1) Investigate the effects of stochastic diffusion in mate-finding in low density populations
2) Determine a threshold number of introduced individuals that enable a population to persist.

METHODS

Assuming that *n* egg masses (each composed of 100-250 eggs of each sex) are introduced in a new area, we coupled the following stochastic processes to model the mating success of the Gypsy Moth.

1- Diffusive dispersal
probability distribution (D=0.003 km²/generation, Shigesada & Kawasaki 1997)
⇩
Where does the larva disperse?

2- Mortality
rate (95%)
⇩
Does the individual survive or not?

3- Emergence time
probability distribution using the GLS model (see "lost in time")
⇩
When does the moth emerge?

4-Mating success
Regression model based on experimental data of release-recapture (Figs. 4a-b) => probability that a male mates a female at a given distance and at a given day after its emergence (on day D).
⇩
Is the female mated?

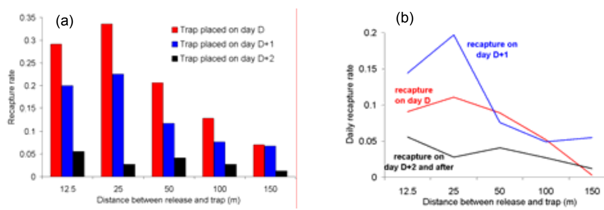

Figure 4: Recapture rates at various distances and various times after the release. (a) Cumulative recapture rates; (b) Daily recapture rates

RESULTS

Since each process was modeled using stochastic simulation, we observed a high variability in the mating success but globally a positive relationship between population density and population growth.

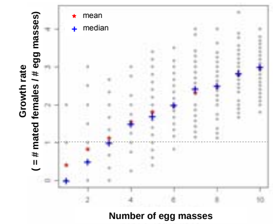

Figure 5: Effects of the number of egg masses introduced on the population growth rate (150 eggs of each sex per egg mass, 50 simulations).

When there were initially 250 eggs of each sex per egg mass (common in low density populations), a strong Allee effect was not detected (growth rate always >1). But when there were 150 eggs of each sex per egg mass (typical of high density populations), we could identify a threshold of 3 egg masses to enable the population to persist (Fig. 5).

DISCUSSION & CONCLUSION

Even though reproductive asynchrony has been mainly considered as an advantage for populations, especially in presence of strong environmental stochasticities, it also may enhance Allee effects and be responsible of populations declines. This temporal isolation of males and females, coupled with the difficulty mates to find each other over space, is a fundamental mechanism underlying the failure of populations to establish.

Allee effects are known to affect the establishment and spread of invading gypsy moth populations (Liebhold and Bascompte 2003, Tobin *et al*. 2006). Our study identifies more precisely the possible causes and describes a spatial gradient in mating success due to a climatic heterogeneity. In comparison to habitat suitability or climatic suitability for completion of gypsy moth development (Gray 2004), mating heterogeneity is quite different and suggests a complementary factor in establishment failure.

References:

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