

Allee effects and pest eradication

Ludek Berec

Department of Biosystematics and Ecology, Institute of
Entomology, Biology Centre ASCR

Institute of Mathematics and Biomathematics, Faculty of
Science, University of South Bohemia

České Budějovice, Czech Republic



INVESTICE DO ROZVOJE VZDĚLÁVÁNÍ

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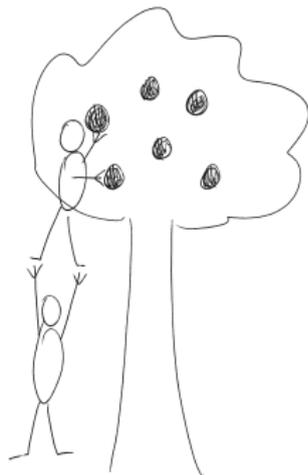
Negative density dependence

Competition



Positive density dependence

Allee effect



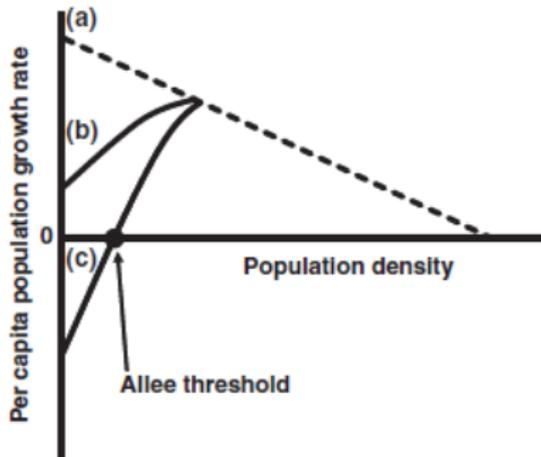
Allee effects occur when **fitness of an individual declines at small population size or low population density**

Individual fitness is commonly quantified as the **per capita population growth rate**, N_{t+1}/N_t

Strong Allee effects

occur when the per capita population growth rate **becomes negative** below a critical size or density

This critical value is known as the **Allee threshold**

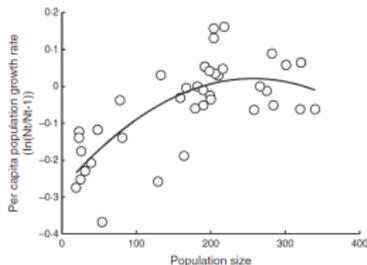


Berec et al. (2007), TREE; Tobin et al. (2011), Ecol. Lett.

Any observed Allee effect has **an underlying mechanism**

Mate-finding Allee effects: difficulty to find a (compatible and receptive) mate at small population size or low population density

Vancouver Island marmot *Marmota vancouverensis*



Berec et al. (2007), TREE; Gascoigne et al. (2009), Popul. Ecol.

Kramer et al. (2009), Popul. Ecol.; Brashares et al. (2010), J. Anim. Ecol.

Simple population model

Discrete-time model of a population with non-overlapping generations, mate-finding Allee effect, and no competitive interactions

$$N_{t+1} = f(N_t) = \lambda N_t P(N_t) = \lambda N_t \frac{N_t}{N_t + \theta}$$

Allee threshold

$$N_{t+1} = N_t = A \quad \Leftrightarrow \quad A = \frac{\theta}{\lambda - 1}$$

$$f'(A) = 2 - \frac{1}{\lambda} > 1 \quad \text{for } \lambda > 1$$

Populations with densities above A grow, while those below A are doomed to extinction

Eradication of small or sparse invading populations

Increasing number of **invading alien species** worldwide

Practicality of eradication (total elimination) is **often questioned**

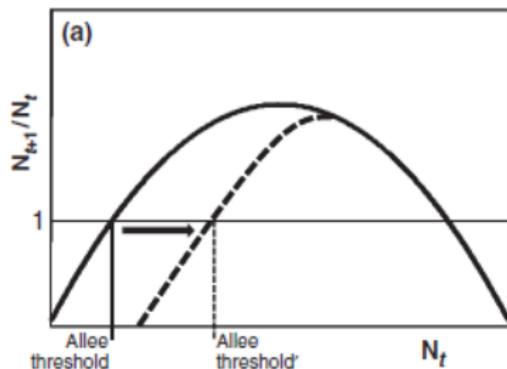
Many questions revolve around the perception of the **difficulty of eliminating every individual** in a population

Related to this is the **difficulty in sampling** very small or sparse populations to confirm that eradication has been accomplished

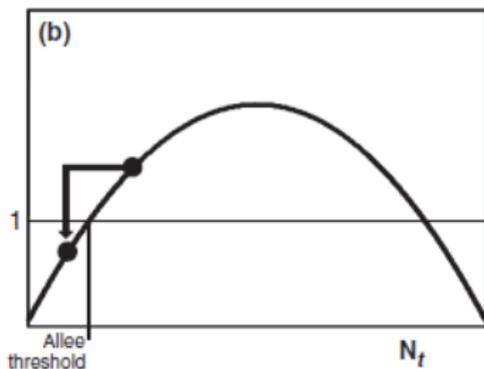
But there are **many successful examples** of eradication

Simberloff (2009), Biol. Invasions; Suckling et al. (2012), J. Econ. Entomol.; Kean et al. (2013), b3.net.nz/gerda

Key to the success of eradication may lie in strong Allee effects that trigger an Allee threshold



Strengthening Allee effect



Lowering population density

Populations that would exceed an Allee threshold in the absence of control tactics could fall below it when the tactics are applied

Pesticide application: prior to reproduction, pesticides are applied that kill a fraction p of individuals



Population model with pesticide application

$$N_{t+1} = \lambda(1-p)N_t \frac{(1-p)N_t}{(1-p)N_t + \theta}$$

Allee threshold

$$N_{t+1} = N_t = A_c \Leftrightarrow A_c(p) = \frac{\theta}{(1-p)[(1-p)\lambda - 1]}$$

$A_c(p)$ increases with p until $p = 1 - 1/\lambda$ (above this value extinction is certain for any N)

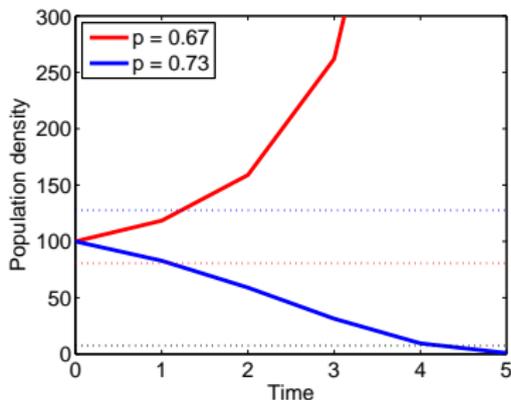
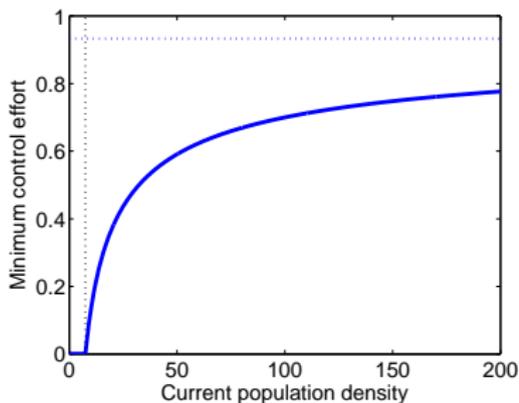
Given current density N we require the next one to fall below $A_c(p)$

$$\lambda(1-p)N \frac{(1-p)N}{(1-p)N + \theta} < A_c(p)$$



Gypsy moth *Lymantria dispar*

$$\lambda = 15 \text{ and } \theta = 105$$



We can stop applying pesticides once N falls below the control-free Allee threshold A

When **two or more tactics** can be used simultaneously, models may help **prioritize control tactics under budget constraints**

FORUM

Combining Tactics to Exploit Allee Effects for Eradication of Alien Insect Populations

DAVID MAXWELL SUCKLING,¹ PATRICK C. TOBIN,² DEBORAH G. McCULLOUGH,³
AND DANIEL A. HERMS⁴

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Bioeconomic synergy between tactics for insect eradication in the presence of Allee effects

**Julie C. Blackwood^{1,2,*}, Ludek Berec³, Takehiko Yamanaka⁴, Rebecca
S. Epanchin-Niell⁵, Alan Hastings⁶ and Andrew M. Liebhold⁷**

Population model

Gypsy moth, or more generally any sexually reproducing insect with non-overlapping generations

Considered control tactics

- 1 Pesticide application affecting larval survival
- 2 Mating disruption via distribution of false pheromone sources

Hybrid modeling approach

- 1 Discrete-time model for between-generation dynamics
- 2 Continuous-time model for mating season dynamics

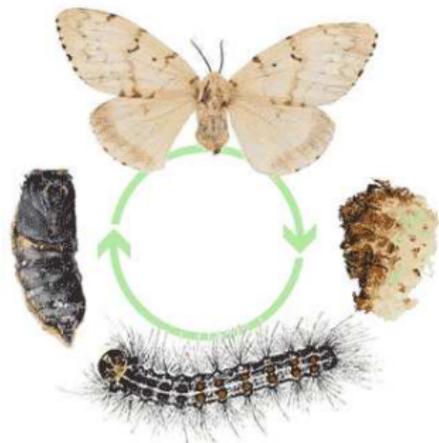
Discrete-time model for **between-generation dynamics**

$J' = J_t m_j p \rightarrow$ egg survival to pupae

$J'' = J' W(J', C, \dots) \rightarrow$ pupal survival

$F_t^m = R(J'', P, \dots) \rightarrow$ mating season model

$J_{t+1} = \lambda F_t^m \rightarrow$ egg production



Predation on pupae: $W(J', C, \dots)$

Holling type II functional response

Daily operation for T days



$$J'_1 = J' \left(1 - \frac{aC}{1 + aT_h J'} \right)$$

$$J'_2 = J'_1 \left(1 - \frac{aC}{1 + aT_h J'_1} \right)$$

...

$$J'' = J'_{T-1} \left(1 - \frac{aC}{1 + aT_h J'_{T-1}} \right)$$

Mating season dynamics: $R(J'', P, \dots)$

Half of pupae emerge as females and half as males

Eclosion times are based on a normal distribution with means μ_M and μ_F and standard deviations σ_M and σ_F for males and females, respectively (protandry: $\mu_M < \mu_F$)

Females mate just once

Five moth states: virgin females (V), fertile males searching for females (M_S), fertile males temporarily resting after mating (M_R), fertile males caught in following false pheromone sources (P_{M_S}), and virgin female–fertile male couples (Q)

The model outputs F_t^m , the **number of females per ha that successfully reproduce** by the end of the mating season

$$\frac{dM_s}{dt} = \frac{1}{2} J'' N(\mu_M, \sigma_M) - z V M_s - y P M_s + \frac{1}{t_r^M} M_r + \dots$$

$$+ \frac{1}{t_p} P_{M_s} + m_F Q + (1 - p^Q) \frac{1}{t^Q} Q - m_M M_s$$

$$\frac{dP_{M_s}}{dt} = y P M_s - \frac{1}{t_p} P_{M_s} - m_M P_{M_s}$$

$$\frac{dM_r}{dt} = p^Q \frac{1}{t^Q} Q - \frac{1}{t_r^M} M_r - m_M M_r$$

$$\frac{dV}{dt} = \frac{1}{2} J'' N(\mu_F, \sigma_F) - z M_s V + m_M Q + (1 - p^Q) \frac{1}{t^Q} C - m_F V$$

$$\frac{dQ}{dt} = z M_s V - \frac{1}{t^Q} Q - (m_M + m_F) Q$$

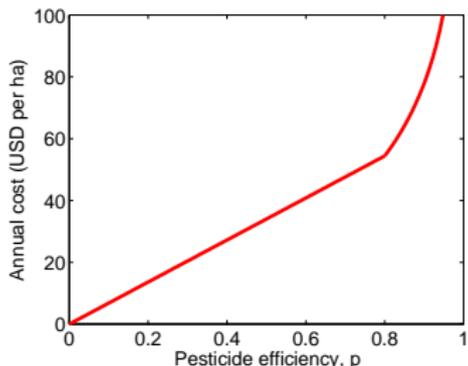
Output variable: $F_t^m = R(J'', P, \dots) = \int_0^T p^Q \frac{1}{t^Q} Q dt$

Annual costs of applying each control tactic per hectare

Pesticide application

Proportion of population killed

$$\text{Cost} = \begin{cases} 54.4 \frac{\ln(1-p)}{\ln(1-0.8)}, & p > 0.8 \\ 54.4 \frac{p}{0.8}, & p \leq 0.8 \end{cases}$$

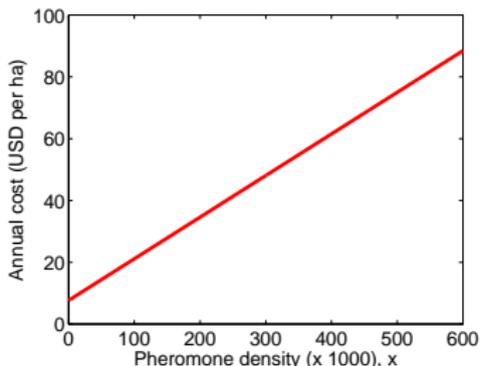


Mating disruption

Number of pheromone flakes / ha

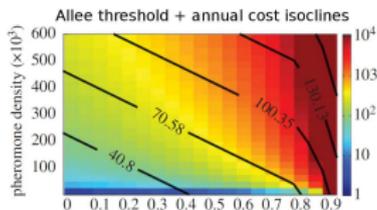
$$\text{Cost} = 7.66 + 1.346 \cdot 10^{-4}x$$

One in every 100 flakes assumed effective in mating disruption: $P = x/100$

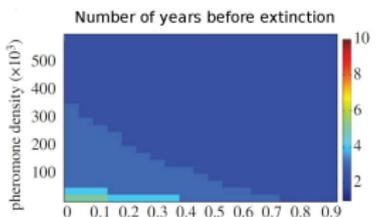


Interaction of pesticide application and mating disruption

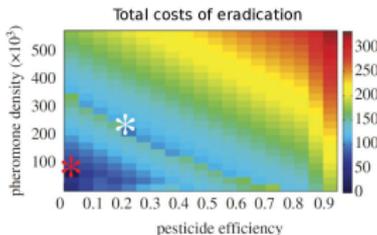
Initial population size = 10 egg masses per hectare



The optimal eradication strategy has a duration of 3 years and requires the application of only false pheromone sources (53.27 USD)



Eradication can be achieved in just 2 years using a combination of both tactics for a modest increase in cost (103.09 USD)



At high enough budgets criteria such as **environmental safety or non-target effect concerns** might be used to select an appropriate combination



Modeling may also **help optimize operations** if complaints about spraying (as happens both with pesticide application and mating disruption) threaten use of the optimal control strategy

Neglecting uncertainty behind Allee effect estimation may generate false predictions of population extinction risk

Luděk Berec and Tomáš Mrkvička

To calculate the Allee threshold we need to know strength of the mate-finding Allee effect θ

θ is estimated from mate-finding experiments

Does using just a point estimate of θ or accounting for uncertainty in its estimate makes any difference for evaluating the probability of population extinction?

Population model

$$N_{t+1} = f(N_t) = \lambda \left(1 - \exp \left(-\frac{N_t}{2\theta} \right) \right) \frac{N_t}{2}$$

Allee threshold

$$N_{t+1} = N_t = A \quad \Leftrightarrow \quad A = -2\theta \ln \left(1 - \frac{2}{\lambda} \right)$$

$$f'(A) = 1 + \left(1 - \frac{\lambda}{2} \right) \ln \left(1 - \frac{2}{\lambda} \right) > 1 \quad \text{for} \quad \frac{\lambda}{2} > 1$$

Populations with densities above A grow, while those below A are doomed to extinction

Mate-finding experiment

Imagine k replicates, in each of which we put together $n_i/2$ males and $n_i/2$ females

Let m_i out of $n_i/2$ females get mated ($i = 1, 2, \dots, k$)

Let $d = (n_1, \dots, n_k, m_1, \dots, m_k)$ be the data vector



Estimating θ : The product binomial likelihood:

$$L(\theta|d) = \prod_{i=1}^k \binom{n_i/2}{m_i} P(n_i/2; \theta)^{m_i} (1 - P(n_i/2; \theta))^{n_i/2 - m_i}$$

Probability of population extinction

Given population density N
and data vector d ,

$$P_{\text{ext}}^1(N) = P(N < A|d) =$$

$$= \int_N^{\infty} p_a(a|d) da =$$

$$= \int_{N/M}^{\infty} p_{\theta}(\theta|d) d\theta =$$

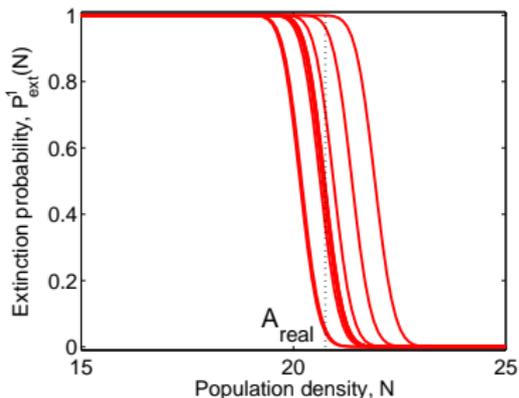
$$= \frac{\int_{N/M}^{\infty} L(\theta|d) p(\theta) d\theta}{\int_0^{\infty} L(\theta|d) p(\theta) d\theta}$$

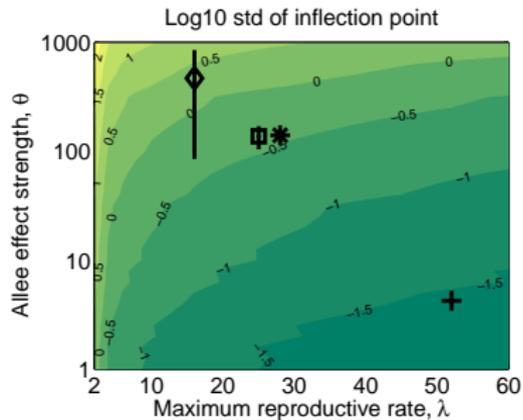
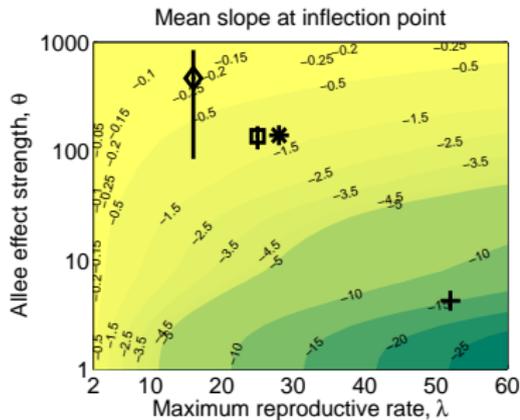
where $M = -2 \ln(1 - 2/\lambda)$

Probability of population extinction **decreases sigmoidally** with increasing population density



Gypsy moth
Lymantria dispar
 $\lambda = 28$ and $\theta = 140$





plus: azuki bean weevil asterisk: gypsy moth
 square: mountain parnassian diamond: freshwater copepod

Uncertainty in the Allee threshold increases when the Allee effect strength increases and the species recovery potential decreases

Not a good news, since we would like to preferentially and efficiently manage slowly recovering populations prone to strong Allee effects

Conclusions

Practically, eradication of a pest population exploiting an Allee effect could proceed as follows:

- 1 Estimate the pest population size or density
- 2 Obtain data for key life history processes to parameterize a model
- 3 Introduce feasible control tactics into the model
- 4 Identify potentially successful control tactics and choose the best tactic(s) based on the available budget

Management of populations subject to Allee effects should be risk averse