

Reproductive Asynchrony in Spatial Population Models: How Mating Behavior Can Modulate Allee Effects Arising from Isolation in Both Space and Time

William F. Fagan,^{1,*} Chris Cosner,² Elise A. Larsen,¹ and Justin M. Calabrese³

1. Department of Biology, University of Maryland, College Park, Maryland 20742; 2. Department of Mathematics, University of Miami, Coral Gables, Florida 33124; 3. Department of Ecological Modeling, Helmholtz Centre for Environmental Research–UFZ, 04318 Leipzig, Germany

Submitted May 11, 2009; Accepted September 26, 2009; Electronically published January 25, 2010

Online enhancements: appendixes, figures.

ABSTRACT: Mate finding, which is essential to both population growth and gene exchange, involves both spatial and temporal components. From a population dynamics perspective, spatial mate-finding problems are well studied, and decreased mate-finding efficiency at low population densities is a well-recognized mechanism for the Allee effect. Temporal aspects of mate finding have been rarely considered, but reproductive asynchrony may engender an Allee effect in which some females go mateless by virtue of temporal isolation. Here we develop and explore a model that unifies previously disparate theoretical considerations of spatial and temporal aspects of mate finding. Specifically, we develop a two-sex reaction-diffusion system to examine the interplay between reproductive asynchrony and the dispersal of individuals out of a patch. We also consider additional behavioral complications, including several alternative functional forms for mating efficiency and advective movements in which males actively seek out females. By calculating the fraction of females expected to go mateless as a joint function of reproductive asynchrony and patch size, we find that the population-level reproductive rates necessary to offset female matelessness may be quite high. These results suggest that Allee effects engendered by reproductive asynchrony will be greatly exacerbated in spatially isolated populations.

Keywords: two-sex population model, critical patch size, mate-searching behavior, age-dependent male reproductive success, density-dependent mating success, demographically effective population density.

Introduction

The process of finding mates is a central theme at the interface of behavior, ecology, and evolution. Mate finding, which is essential to both population growth and the exchange of genes, involves both spatial and temporal com-

ponents. Researchers have identified many empirical examples in which both spatial and temporal components of mate finding are important, and the underlying issues are particularly well studied in butterflies and moths (Wells et al. 1990; Roland et al. 2000; Dennis and Shreeve 2008; Ovaskainen et al. 2008; Robinet et al. 2008) and insects more generally (Waldbauer 1978; Hopper and Roush 1993). In addition, many plants face similar reproductive issues that reflect a combination of reproductive timing and spatial location (e.g., tropical plants that occur in very low densities and flower asynchronously; Augspurger 1981; Bullock and Bawa 1981).

From the perspective of population dynamics, spatial problems of finding mates are well studied (Wells et al. 1990; Veit and Lewis 1996; Boukal and Berec 2002), and decreased mate-finding efficiency at low population densities is a well-recognized mechanism for the Allee effect (McCarthy 1997; Courchamp et al. 2008). Temporal aspects of mate finding have also been considered but to a far more limited extent. For example, models of small-population dynamics have demonstrated that reproductive asynchrony may engender an Allee effect in which some females go mateless by virtue of temporal isolation (Calabrese and Fagan 2004; Calabrese et al. 2008). In those models, neither of which considered spatial dynamics, decreased temporal overlap with potential mates translates into an increasing proportion of females failing to mate when asynchrony increases in populations of a fixed size or when population size decreases in populations with a fixed degree of asynchrony. Collectively, theoretical models suggest that asynchrony can be costly at low density, even though asynchrony can be strongly selected for as an effective bet-hedging strategy in the face of environmental unpredictability in high-density populations (Iwasa 1991; Iwasa and Levin 1995).

Here we develop and explore a model that allows us to

* Corresponding author; e-mail: bfagan@umd.edu.

unify the previously disparate theoretical considerations of spatial and temporal aspects of mate finding (but see Robinet et al. [2008], who considered an invasion dynamics scenario). In our efforts, we emphasize the joint effects of spatial isolation and temporal asynchrony on population dynamics for a population that lives in a discrete patch of habitat. We also consider how the details of mating behavior may change the results. Starting from an established model of reproductive timing, we develop a two-sex reaction-diffusion system to explore the interplay between reproductive asynchrony and loss of individuals across the edges of a patch. Using both an analytical approximation and numerical solutions, we calculate the expected fraction of mateless females as a joint function of reproductive asynchrony and patch size. We also consider additional complications, including the adoption of detailed, empirically supported functional forms for mating efficiency and the introduction of an advection term for the case in which males actively seek out females. Throughout these various scenarios, we find that the population-level reproductive rates necessary to offset female matelessness arising from the joint effects of reproductive asynchrony and spatial loss may be prohibitively high. These results suggest that Allee effects driven by reproductive asynchrony will be greatly exacerbated in spatially isolated populations.

Methods

A Reproductive-Timing Model

As summarized by Calabrese et al. (2008), an ecological model with reproductive asynchrony must have three fundamental features: (1) individuals must, on average, be available to mate for only a fraction of the population-level breeding period; (2) females are not guaranteed to mate before they die; and (3) population density of both males and females must be explicitly modeled throughout the reproductive activity period. One model meeting these requirements can be written as the nonautonomous system

$$\frac{dM}{dt} = M_0 g(t, \theta_m) - \alpha_m M, \quad (1a)$$

$$\frac{dF}{dt} = F_0 g(t, \theta_f) - \alpha_f F, \quad (1b)$$

where t is time (days); M_0 and F_0 are total densities of males and females, respectively; $g(t, \theta)$ is a probability distribution, with parameter vector θ dictating how emergence events (alternatively, maturation events) are spread over time during the breeding season; and α is a constant per-day death rate (Calabrese et al. 2008). The subscripts allow parameters to differ between males (m) and females

(f) within the population. This is the same general emergence and death model that was originally introduced by Manly (1974) and studied extensively in the context of protandry (e.g., Zonneveld and Metz 1991; Zonneveld 1992).

We use the standard and widely applicable kinetic approach to describe mate encounter, assuming that the number of matings per unit time is proportional to the product of male and unmated female densities (Wiklund and Fagerström 1977; Wells et al. 1990; Zonneveld and Metz 1991; Zonneveld 1992; Hutchinson and Waser 2007). We assume that females are monandrous and that males may mate many times. The rate of change in the density of unmated females, denoted U , is then

$$\frac{dU}{dt} = F_0 g(t, \theta_f) - c(\bullet)MU - \alpha_f U, \quad (2)$$

where $c(\bullet)$ is a function representing the instantaneous mating rate (efficiency) and captures species-specific details of mating biology. The cumulative density of mated females at any time, $R(t)$, is given by the solution to

$$\frac{dR}{dt} = c(\bullet)MU. \quad (3)$$

We assume that all population dynamics take place within a season of length T , which we set at a default value of $T = 150$ days, allowing us to explore a wide range of asynchrony scenarios. We are interested in the total season-long proportion of females that die mateless, which can be calculated as

$$q^* = 1 - \frac{R(T)}{F_0}. \quad (4)$$

Adding Explicit Space

To add explicit space to the above model of reproductive asynchrony (eqq. [1]–[3]), we envision a population of animals inhabiting a one-dimensional discrete patch. Butterfly case studies were used as empirical examples in earlier papers on reproductive timing (e.g., Wiklund and Fagerström 1977; Wells et al. 1990; Zonneveld and Metz 1991; Calabrese and Fagan 2004; Calabrese et al. 2008), and we follow that approach here, envisioning, as an example, a population of butterflies inhabiting an alpine meadow.

We assume that all males and females move according to the same diffusion process; however, we assume that every mated female will, immediately after mating, lay all her eggs inside the patch. In our analyses of population

dynamics, this represents a conservative assumption that will cause all offspring from successful matings to be retained locally. With these assumptions about movement, our system of equations applied to a one-dimensional patch of length L becomes

$$\frac{\partial M}{\partial t} = M_0 g(t, \theta_m) - \alpha_m M + D \frac{\partial^2 M}{\partial x^2}, \tag{5a}$$

$$\frac{\partial F}{\partial t} = F_0 g(t, \theta_f) - \alpha_f F + D \frac{\partial^2 F}{\partial x^2}, \tag{5b}$$

$$\frac{\partial U}{\partial t} = F_0 g(t, \theta_f) - c(\bullet)MU - \alpha_f U + D \frac{\partial^2 U}{\partial x^2}, \tag{5c}$$

$$\frac{\partial R}{\partial t} = c(\bullet)MU, \tag{5d}$$

where D is a diffusion coefficient with units space²/time. Equations (5) have Dirichlet (absorbing) boundary conditions on the patch edges,

$$\begin{aligned} M(t, 0) = M(t, L) = F(t, 0) = F(t, L) = \\ U(t, 0) = U(t, L) = R(t, 0) = R(t, L) = 0, \end{aligned} \tag{6}$$

and population densities that are initially 0 everywhere,

$$M(0, x) = F(0, x) = U(0, x) = R(0, x) = 0. \tag{7}$$

These boundary conditions assume that any individual emigrating from the patch is lost to that local population. (Note, however, that these boundary conditions do not necessarily imply that emigrants are dead, meaning that, in another context, a metapopulation perspective could be appropriate and could yield different insights.) Animal behaviors near habitat edges can be quite complicated (for reviews, see Fagan et al. 1999; Ries et al. 2004), and the edge-related behaviors of butterflies have been particularly well studied (Kuussaari et al. 1998; Roland et al. 2000; Schultz and Crone 2001; Crone and Schultz 2008). If instead of absorbing boundaries we used partially reflecting boundary conditions, we would generally expect similar effects of space but with a lower loss rate due to emigration.

The formula for proportion of unmated females on a patch of size L becomes

$$q_{\text{spatial}}^* = 1 - \frac{\int_{x=0}^{x=L} R(T, x) dx}{F_0 L}. \tag{8}$$

In later sections, we will solve the system of equations (5)–(7) both via a Fourier approximation and numerically.

Adding Active Searching for Mates

Animal movement behaviors may be far more sophisticated than the idealized random behaviors represented by diffusion. In insects, searching for mates may be aided by chemical cues (pheromones) that serve to attract males toward females (e.g., Barrows 1975; Landolt and Phillips 1997), and males may seek out prominent landscape features, such as hilltops, from long distance (Dennis and Shreeve 2008). Additionally, males may actively pursue females visually detected from some distance. For example, Rutowski et al. (2001) demonstrate that perched territorial males of the nymphalid butterfly *Asterocampa leilia* may respond to females in flight up to 3 m away. To capture these kinds of movement behaviors, we modified equation (5a) to introduce a term for advective movement in addition to random diffusive movement. This complication allows males to move up a spatial gradient of females, yielding

$$\frac{\partial M}{\partial t} = M_0 g(t, \theta_m) - \alpha_m M + D \frac{\partial^2 M}{\partial x^2} - B_f \frac{\partial}{\partial x} \left(M \frac{\partial F}{\partial x} \right), \tag{9}$$

where the coefficient B_f is the rate of advection up a density gradient of females. Alternatively, males might be able to discriminate between mated and unmated females (Labine 1964; Schiestl and Ayasse 2000) and would move toward only unmated females. In that case, the appropriate formulation is

$$\frac{\partial M}{\partial t} = M_0 g(t, \theta_m) - \alpha_m M + D \frac{\partial^2 M}{\partial x^2} - B_u \frac{\partial}{\partial x} \left(M \frac{\partial U}{\partial x} \right), \tag{10}$$

where the coefficient B_u is the rate of advection up a density gradient of unmated females. In “Results,” we report on cases both with and without advective movement.

An Analytical Approximation

In appendix A in the online edition of the *American Naturalist*, we present analytical solutions to the spatial model (eqq. [5], [6]) using a standard Fourier series approach. To a first approximation, we can replace each equation in the spatial model with an ordinary differential equation that facilitates analysis but at the cost of ignoring the details of spatial dynamics.

*Specifying Functions for the Emergence
Distribution and Mating Rate*

In asynchronous populations, the shape of the emergence distribution may modulate the effects of asynchrony by influencing the tendency of individuals to become isolated in time from one another (Calabrese and Fagan 2004). Following Calabrese et al. (2008), we use the gamma distribution to model emergence times because it is flexible in shape, has a bounded left tail that provides a defined “start point” to the populations’ reproductive activity, and is relatively parameter sparse. The gamma probability density function is

$$g(t, \theta) = \frac{\lambda}{\Gamma(\mu)} (\lambda t)^{\mu-1} \exp(-\lambda t), \quad (11)$$

where $\theta = (\lambda, \mu)$, λ is the inverse scale parameter, μ is the shape parameter, and $\Gamma(\mu)$ is the gamma function. Here, we assume $\theta_f = \theta_m = \theta$ and no protandry, leaving investigations of the interplay between protandry and reproductive asynchrony in a spatial setting for a later article. Following results from Calabrese et al. (2008), we hold $\mu = 5$ throughout this article and manipulate the level of asynchrony in the population by varying λ (fig. 1). For a lower threshold, we set $\lambda = 0.10$ throughout, which is the most asynchronous the population can be and still have emergence finish within our $T = 150$ -day season (technically, for $\lambda = 0.10$, 99.91% of the population emerges within 150 days). For $\lambda > 0.15$, all emergence concludes by $t = 100$.

Recent studies have highlighted the potential importance of behavioral features such as age-dependent male reproductive success (Kemp et al. 2006) and density-dependent mating success (Kokko and Rankin 2006) for population dynamics. To explore these issues in the context of an asynchronously reproducing population, we considered four scenarios for the mating rate function $c(\bullet)$. First, and simplest, we set the mating rate to be a constant

$$c(\bullet) = c_0 = 0.1. \quad (12)$$

For the remaining three scenarios, we adopted mating rate functions that each received strong empirical support (from among 10 candidate functions) in a time series analysis of mating behavior by butterflies in the genus *Parnassius* (Calabrese et al. 2008). These models were (1) male age:

$$c(\bullet) = c(t, c_1) = c_1 \bar{a}_m(t); \quad (13a)$$

(2) inverse male age:

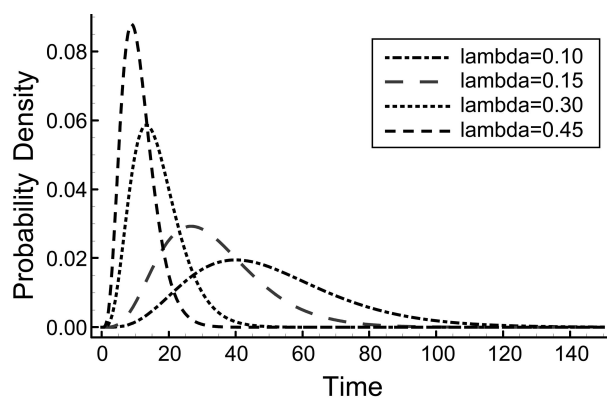


Figure 1: Reproductive asynchrony as determined by λ , the inverse scale parameter of the gamma distribution (eq. [11]). Small values of λ lead to more asynchronous reproduction. For all curves, $\mu = 5$. Note that time on the X-axis is time to emergence or time to the onset of reproductive maturity.

$$c(\bullet) = c(t, c_2) = \frac{c_2}{1 + \bar{a}_m(t)}; \quad (13b)$$

and (3) inverse male density:

$$c(\bullet) = c(t, x, c_3) = \frac{c_3}{(1 + M(t, x))}. \quad (13c)$$

In equations (13a) and (13b), $\bar{a}_m(t)$ is the mean age of males alive at time t during the breeding season. Following Calabrese et al. (2008), we have for the gamma distribution (eq. [11])

$$\bar{a}_m(t) = \int_0^t a \frac{g(t-a, \theta_m) \exp(-\alpha_m a)}{\int_0^t g(t-z, \theta_m) \exp(-\alpha_m z) dz} da. \quad (14)$$

To facilitate comparisons among different $c(\bullet)$ functions, we find values of the constants c_* (c_1 , c_2 , or c_3 as appropriate) such that the time averages of all the functions across the breeding season are equal to $c_0 = 0.1$, which is based on the empirical findings of Calabrese et al. (2008). Note that all three alternative mating functions can be written as a product of a constant c_* and a time-varying function $f(t)$. The appropriate constant can then be calculated as

$$c_* = \frac{c_0 T}{\int_0^T f(t) dt}. \quad (15)$$

Quantifying Critical Patch Size

To explore how variation in patch size scales the effects of diffusive loss of individuals across patch boundaries on population persistence, we must specify a population growth process. Following Calabrese and Fagan (2004), we assume that the population within a patch grows geometrically across breeding seasons:

$$N_{t+1} = \delta N_t(1 - q_{\text{spatial}}^*), \tag{16}$$

where N is female population density and δ is the finite rate of increase under perfect mate-finding conditions. The population will become extinct when

$$q_{\text{spatial}}^* > \frac{\delta - 1}{\delta}. \tag{17}$$

To quantify the effect of a given combination of asynchrony, diffusion, and patch size on population dynamics, we calculate δ^* , the minimum geometric growth rate that will allow indefinite population persistence, as

$$\delta^* = \frac{-1}{q^* - 1} = \frac{F_0 L}{\int_{x=0}^{x=L} R(T, x) dx}. \tag{18}$$

Numerical Solutions

All numerical solutions to partial differential equation systems were calculated in Mathematica, version 6.0, using the function `NDSolve[]`. For solutions to our simple-diffusion systems (eqq. [5]), we were able to call this function with default options. However, to avoid numerical instabilities that are typical of partial differential equations containing both diffusive and advective components, we solved systems including equations (9) and (10) using a very small step size ($t = 0.02$).

Results

The analytical approximation (app. A) to the full partial differential equation system illustrates the key qualitative result that relative to reproductive asynchrony alone, adding dispersal-mediated losses across the patch edges increases the fraction of the female population that fails to mate (fig. 2). Though the analytical approximation consistently gets the correct qualitative answer, it is quantitatively more accurate in more asynchronous populations (fig. 2). In other words, the higher-order Fourier terms that have been dropped from the approximation are more important in synchronous populations (large λ) than in asynchronous populations. This dependence on λ occurs

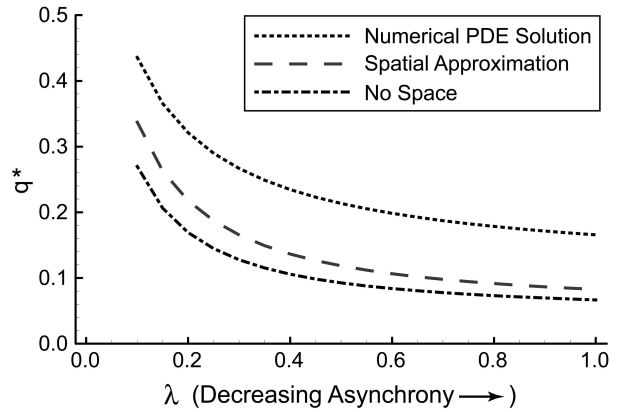


Figure 2: Comparison of cumulative female matelessness (q^*) as a function of reproductive asynchrony for a nonspatial model (eqq. [1]–[4]) and the spatial model (eqq. [5]) as determined by an analytical approximation (app. A in the online edition of the *American Naturalist*) and a numerical solution. For all curves, $c(\bullet) = c_0 = 0.1$, $\mu = 5$, $\alpha_f = \alpha_m = 0.2$, and $M_0 = F_0 = 100$. For this and all subsequent figures, note that small values of λ correspond to high levels of asynchrony and that as λ increases, the population becomes more synchronous.

because in more synchronized populations, the population dynamics are concentrated in a narrow period of time during the season and the higher-order terms, which take some time to decay away, play more of a role when the dynamics are concentrated in a narrow period. Consequently, the spatial effects are not uniform across parameter space, and this attempt to approximate diffusion by a constant loss term will miss key aspects of the results that are visible only via a consideration of spatial dynamics.

The interplay between reproductive asynchrony and diffusion-mediated loss across the patch edges determines cumulative female matelessness (q^*) in the spatial model (eqq. [5]). High levels of asynchrony (small λ) coupled with fast diffusion lead to large fractions of the female population going mateless (sometimes >50%; fig. 3A). Even for well-synchronized populations that would not normally experience a decrease in population reproductive capacity due to asynchrony, losses across the patch boundary can induce female matelessness. Calculation of a spatial loss multiplier (the ratio $q_{\text{spatial}}^*/q_{\text{nonspatial}}^*$; fig. 3B) and a measure of additive spatial loss ($q_{\text{spatial}}^* - q_{\text{nonspatial}}^*$; fig. 3C) illustrate the substantial extent to which spatial effects can aggravate matelessness due to asynchrony. For much of the $\lambda \times D$ parameter space that we considered here, the addition of dispersal (as simple diffusion) more than doubles the fraction of females that go mateless over their lifetimes compared to those in the corresponding asynchrony-only model (fig. 3B).

To assure population persistence, the population growth

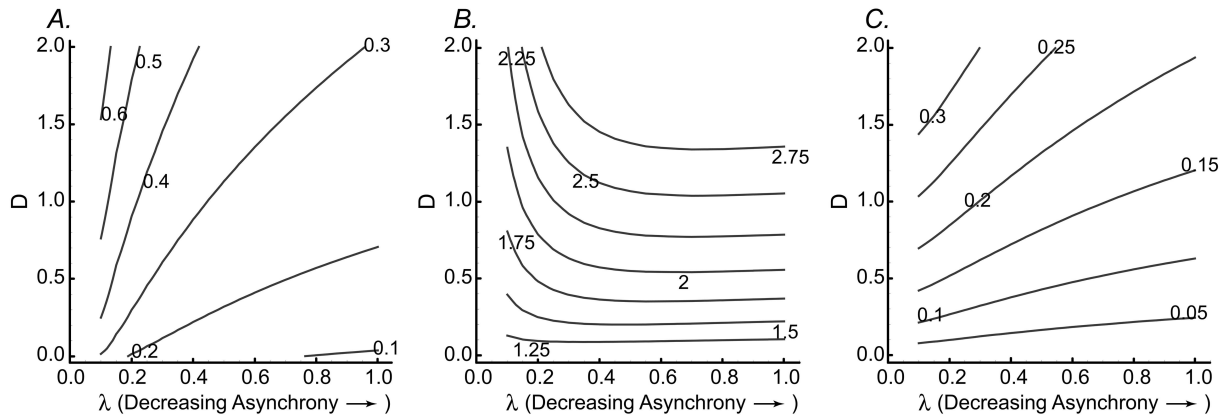


Figure 3: Preliminary summary of how the interplay between reproductive asynchrony and diffusion-mediated loss across habitat edges determines cumulative female matelessness (q^*). A, Surface contours are q^* ; the case $D = 0$ corresponds to the nonspatial model (eqq. [1]–[4]). B, Surface contours are a spatial loss multiplier, that is, the ratio $q_{\text{spatial}}^*/q_{\text{nonspatial}}^*$. C, Surface contours are additive spatial loss, that is, the difference $q_{\text{spatial}}^* - q_{\text{nonspatial}}^*$. Parameters are $c^*(\bullet) = c_0 = 0.1$, $\mu = 5$, $\alpha_f = \alpha_m = 0.2$, $M_0 = F_0 = 100$, and $L = 10$.

rate, δ^* , must be sufficiently large to offset matelessness arising from the joint effects of reproductive asynchrony and the loss of individuals across the patch boundaries. Accordingly, for a given δ^* , we can determine the critical patch size above which persistence is possible; framed this way, critical patch size is a function of the degree of asynchrony. Figure 4, where δ^* is plotted as a series of contours, demonstrates that in the absence of dispersal, thresholds for population persistence depend only on asynchrony (fig. 4A), whereas for the case of simple diffusion (eqq. [5]), the critical patch size for a given population growth rate increases monotonically as population asynchrony increases (fig. 4B–4D). As diffusion increases, the value of δ^* necessary to assure persistence for any given combination of patch size and asynchrony increases (fig. 4B–4D). The preceding results can also be visualized in terms of classical Allee effect plots, in which population growth rate is plotted against population density (app. B in the online edition of the *American Naturalist*).

Male movements that are biased toward females can either enhance or reduce female reproductive success, depending on the details (fig. 5). Male movement toward unmated females is always beneficial and partially counteracts the negative effects of diffusive loss. In figure 5A, 5C, contours plotted are the reduction in δ^* afforded by male advection toward unmated females (i.e., $\delta_D^* - \delta_{D+B_U}^*$). Male advection toward unmated females is most advantageous for small patches, where the risk of dispersing out of the patch is larger, and in highly asynchronous populations, where the risk of going mateless due to isolation in time is larger. The benefits of such male movement toward unmated females decrease with higher diffusion (D) because the advective movement acts to strongly offset

the risk of males diffusing out of the patch, which increases their opportunities for co-occurring with unmated females (fig. 5A, 5C).

Interestingly, when males cannot reliably discern female mating status, biased movement toward females may either increase or decrease δ^* , depending on the circumstances. This effect can be easily seen by contrasting figure 5B and figure 5D, which plot contours of $\delta_D^* - \delta_{D+B_F}^*$. Advection toward all females is most advantageous for very small patches with highly asynchronous populations, and this result does not depend on the diffusion rate. However, as patch size increases and as populations become more synchronized, advection toward all females regardless of mating status can become decidedly disadvantageous if the diffusion rate is high (fig. 5D), increasing matelessness and increasing the population growth rate δ^* necessary to overcome loss of reproductive individuals. This switch from advantageous to disadvantageous advection can be seen in figure 5D as the contours of $\delta_D^* - \delta_{D+B_F}^*$ switch from positive to negative values. These effects on δ^* can also be framed a different way. If population growth rate is held constant in synchronous populations in large patches, biased male movement toward all females results in substantially larger critical patch sizes than for either the “purely random movement” scenario or the “attraction to unmated females” scenario.

Changing from a constant mating rate (c_0) to more complicated (and perhaps more biologically realistic) mating rate functions that varied over time (eqq. [13]) had substantial impacts on the population growth rate δ^* necessary to overcome the loss of reproductive individuals due to the joint effects of asynchrony and emigration (fig. 6). When mating efficiency depended directly on male age

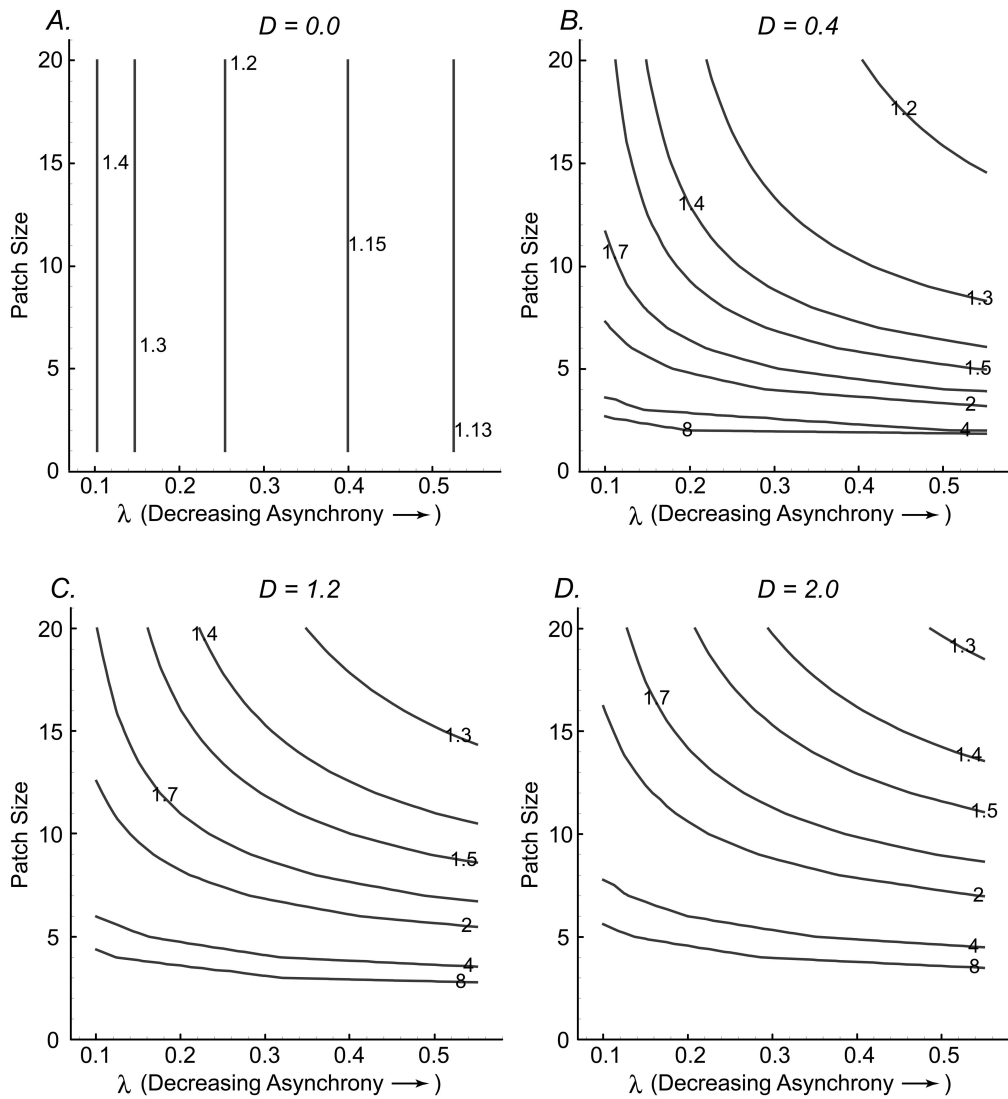


Figure 4: Contours of geometric population growth rate δ^* necessary for population persistence (eq. [18]) as functions of the degree of asynchrony λ and patch size L for the case of simple diffusion (eq. [5]). In A, where there is no dispersal, δ^* depends only on the degree of asynchrony in the population, λ . As diffusion increases (B–D), conditions for persistence become increasingly stringent for a given combination of asynchrony and patch size. For a given population growth rate, the critical patch size necessary for population persistence increases nonlinearly as asynchrony increases (smaller λ) and as diffusion increases. Parameters are $c^* = c_0 = 0.1$, $\mu = 5$, $\alpha_i = \alpha_m = 0.2$, and $M_0 = F_0 = 100$.

(eq. [13a]), δ^* was higher for all parameter combinations we considered than was the corresponding δ^* for the case of constant mating efficiency (cf. fig. 6A and fig. 6B). In addition, having mating efficiency depend directly on male age introduced a striking nonmonotonicity in the δ^* contours such that when reproductive rate was held constant, populations with intermediate levels of reproductive asynchrony had lower critical patch sizes than did populations with greater or lesser degrees of asynchrony (fig. 6B). This nonmonotonicity occurred only for relatively large patch

sizes, where diffusive losses across the patch boundaries would be minimized.

When mating efficiency depended on inverse male age (eq. [13b]), critical patch size contours were again consistently decreasing functions of reproductive synchrony. However, having mating efficiency depend on inverse male age resulted in δ^* values that were lower than the corresponding δ^* values for the case of constant mating efficiency (cf. fig. 6A and fig. 6C). This was especially true in relatively synchronized populations in large patches. Last,

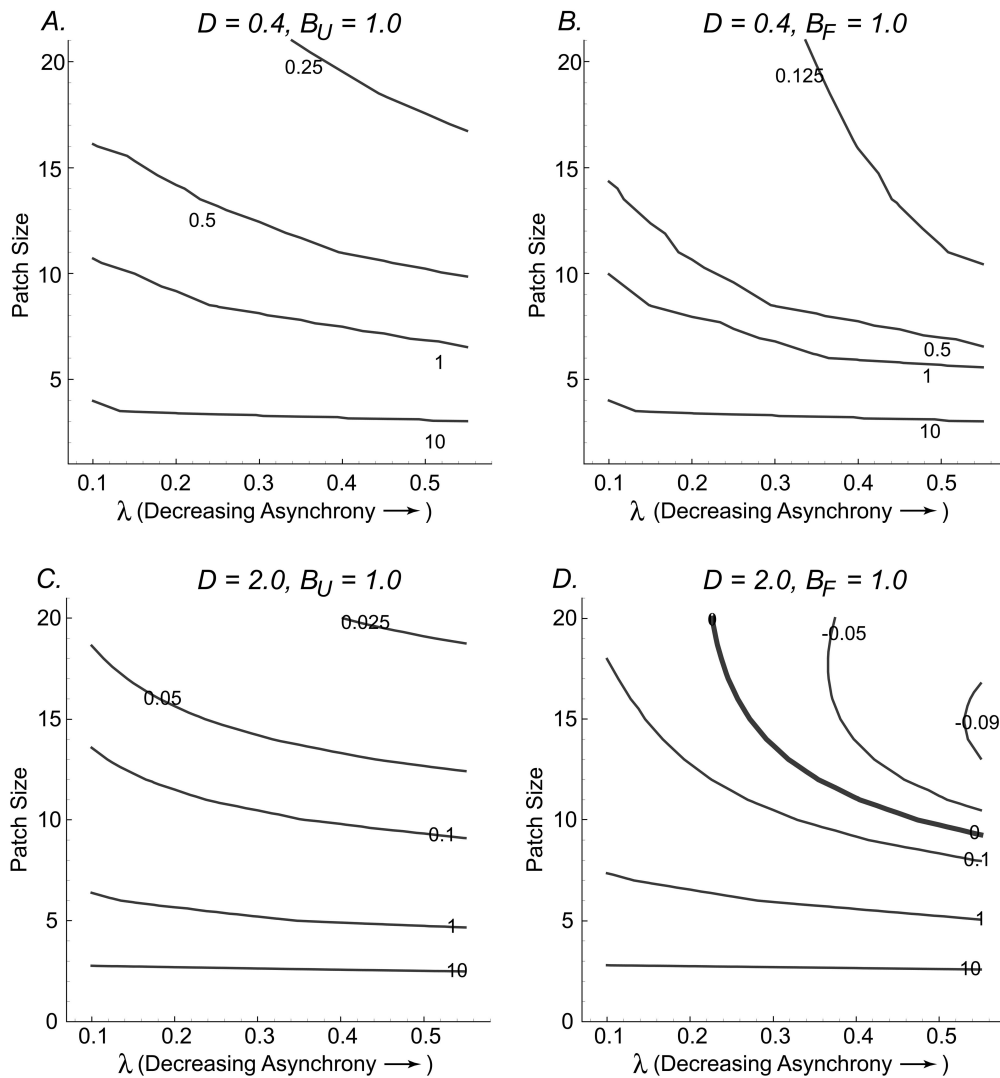


Figure 5: Contours of the difference in geometric population growth rate δ^* necessary for population persistence (eq. [18]) as functions of the degree of asynchrony λ and patch size L for contrasting pairs of male movement behaviors. Panels plot the difference in population growth rate between the simple male diffusion case (eq. [5a]) and the case of simple diffusion plus male advection toward females (eqq. [9], [10]). A and C plot $\delta_D^* - \delta_{D+B_U}^*$ for the case of male advection toward unmated females, whereas B and D plot $\delta_D^* - \delta_{D+B_F}^*$ for the case of male advection toward all females regardless of mating status. Positive values of these differences (e.g., A–C) mean that advection is advantageous to population persistence because it allows for a lower-threshold population growth rate to offset reproductive losses due to the joint effects of asynchrony and emigration. In D, however, both positive and negative values of $\delta_D^* - \delta_{D+B_F}^*$ appear, meaning that advection can have both positive and negative impacts on the thresholds for population persistence, depending on the particular combination of patch size and reproductive asynchrony involved. Parameters are $\alpha^* = c_0 = 0.1$, $\mu = 5$, $\alpha_f = \alpha_m = 0.2$, and $M_0 = F_0 = 100$.

when mating efficiency depended on inverse male density (eq. [13c]), the model yielded major increases in δ^* relative to the case of constant mating efficiency. Moreover, the shape of the critical patch size contours changed qualitatively in this final behavioral scenario. Unlike the previous three cases, where critical patch size tended to increase with increasing asynchrony, when mating efficiency depended on inverse male density, the minimum critical

patch size (for a given population growth rate) occurred for the most asynchronous populations (fig. 6D).

Discussion

In this study, we introduced a modeling framework that permits a unified approach to the theoretical study of mate-finding behavior from spatial and temporal per-

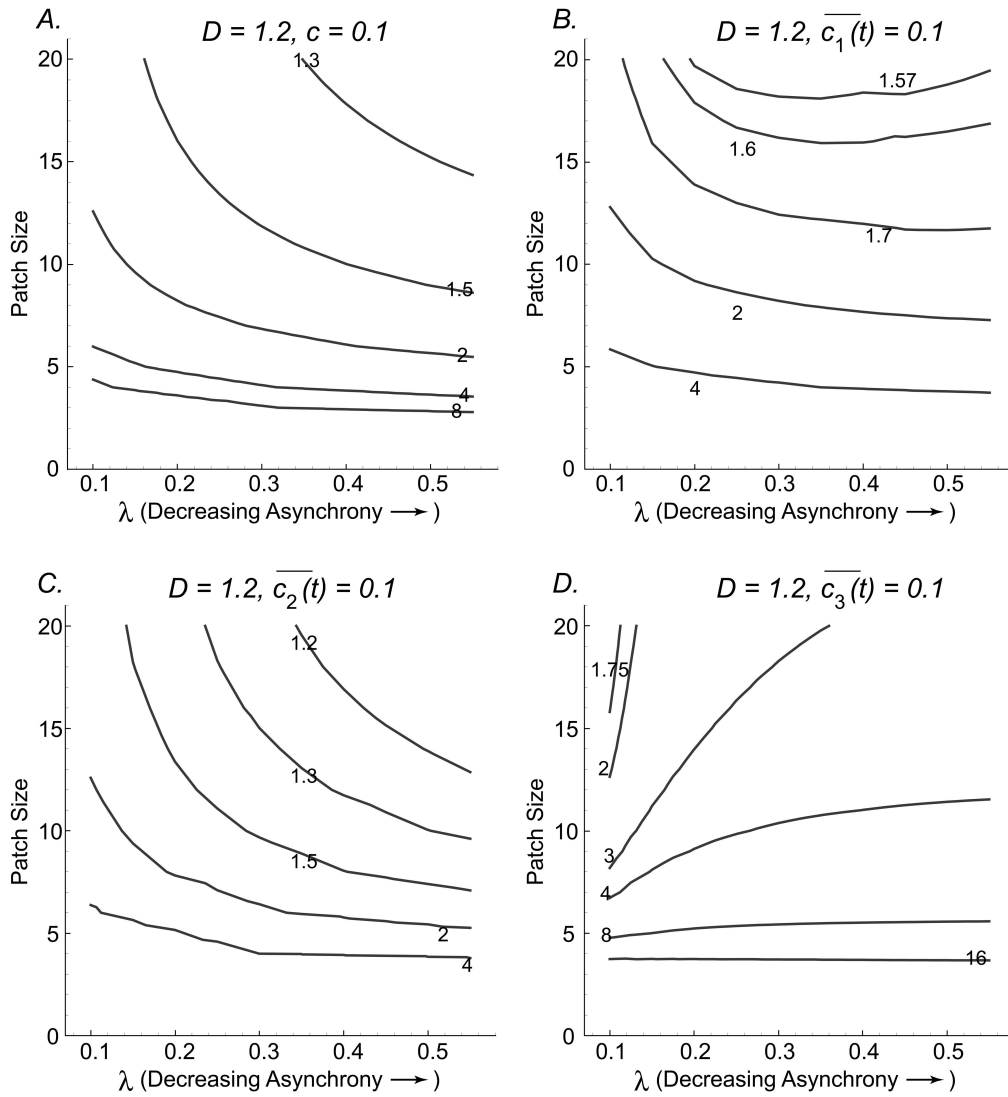


Figure 6: Contours of geometric population growth rate δ^* necessary for population persistence (eq. [18]) as functions of the degree of asynchrony λ and patch size L for the case of simple diffusion (eqq. [5]) using alternative mating-efficiency functions (eqq. [13]). In A, we set the mating rate to be a constant $c(\bullet) = c_0 = 0.1$. In B, instantaneous mating rate increases with male age (eq. [13a]). Note the nonmonotone contours in upper right. In C, instantaneous mating rate is inversely related to male age (eq. [13b]). In D, instantaneous mating rate is inversely related to male density (eq. [13c]). Parameters are $\mu = 5$, $\alpha_f = \alpha_m = 0.2$, and $M_0 = F_0 = 100$.

spectives. We specifically focused on the joint effects of reproductive asynchrony and dispersal on population persistence in a model setup where increased movement can lead to increased emigration from a patch. Acting together, asynchrony and dispersal increased the fraction of females in a population that go mateless (fig. 3), which translated into harsher conditions for population persistence, as an increased population growth rate was necessary to offset loss of reproductive potential due to isolation in time and emigration (fig. 4). Similar findings have been reported by Robinet et al. (2008), who demonstrated that repro-

ductive asynchrony in low-density populations can inhibit the spatial spread of an invading population.

Extending our treatment of male movement behavior beyond simple diffusion to include advection toward females qualitatively changed the outcome of the model (fig. 5). Whether male attraction toward females provided a net benefit to the population (i.e., whether attraction reduced the threshold population growth rate necessary for population persistence) depended sensitively on whether males could differentiate mated from unmated females. When males could not discern females' mating status, male ad-

vection toward females actually increased female matelessness relative to the simple-diffusion case for a wide range of parameter combinations (fig. 5B, 5D). This is a rather counterintuitive result, but it appears to occur because the advection tends to draw males toward the center of the patch, thereby allowing some females to die mateless within the patch and also allowing some unmated females to emigrate from the patch (app. C in the online edition of the *American Naturalist*).

The extent to which males can actively discern females' mating status made a substantial difference in this model (fig. 5). Schiestl and Ayasse (2000) demonstrated that a postmating odor released by mated female andrenid bees dissuaded male mating attempts; however, it is not clear how widespread pheromonal cues related to mating status are among insects. Nevertheless, even if males are unable to discern differences between mated and unmated females from a distance, females may employ behavioral mechanisms (e.g., altered flight patterns, postural changes) to actively resist courting males (Labine 1964), and these may feed back to alter male movements in flight. Yamanaka and Liebhold (2009) discuss how false attractants that lure males away from unmated females can lead to decreased mating success.

As was the case for the models with different assumptions about movement, models featuring different assumptions about reproductive dynamics induced major qualitative changes in the relationship between critical patch size and reproductive asynchrony (fig. 6). In addition to constant mating efficiency, we considered three behavioral scenarios that received substantial empirical support in an analysis of butterfly reproductive dynamics (Calabrese et al. 2008). These scenarios involved relatively subtle biological details—specifically, dependence of mating success on male age or density—that would be exceedingly difficult to discern in field studies of butterfly populations. Nevertheless, these alternative behavioral scenarios determined whether, for populations with a fixed reproductive rate, critical patch size was a decreasing, increasing, or nonmonotone function of reproductive asynchrony (fig. 6). Because these qualitative differences in the relationship between critical patch size and reproductive asynchrony occurred even though the season-long average mating efficiency was held constant across all four behavioral scenarios (fig. 6), this is a striking demonstration of how sensitive results in spatial ecological models can be to behavioral details, which are unfortunately absent from many models.

We ourselves are guilty of minimizing behavior in our models to keep them as simple as possible yet still make our points. For example, we assumed that the diffusion rates for male and female butterflies were the same in any given population. However, male and female butterflies

may fly at different speeds or for different periods of time, resulting in strong heterogeneities in dispersal abilities among individuals (Hanski et al. 2004). Across more than 40 species, the extent to which males and females of a species differ in flight abilities appears linked to the mating strategy employed by the males (e.g., perching vs. patrolling males; Wickman 1992). In some species, sex-specific differences in flight performance and wing kinematics are tied to differences in flight morphology (Gilchrist 1990; Berwaerts et al. 2006). In contrast, in other species, females exhibit different behavioral strategies for movement than do males (e.g., females may be highly cryptic and spend part of their time crawling through vegetation; Roland et al. 2000). Boundary dynamics may also differ between the sexes. In some species, females appear less willing to exit a habitat patch than do males (Ovaskainen et al. 2008). Such reduced emigration by females would increase the fraction of females mated within a patch, thereby reducing critical patch sizes evident in figures 4 and 5. Such real-world complications would be worth pursuing in subsequent work.

Another topic for further exploration concerns our assumption that males and females exhibit equivalent mortality rates. While one could explore the simple case of $\alpha_f \neq \alpha_m$ using the present model, it may not be sufficient to capture the kinds of intersexual differences in mortality patterns evident in nature. For example, Wiklund et al. (2003) have demonstrated that the relative life span of male and female butterflies differs among species as a function of mating system, with males in polyandrous species having relatively longer life spans. Here, we have assumed monandry, and an exploration of the joint effects of reproductive asynchrony and dispersal in a polyandrous species would require a rather significant reformulation of the model, probably following the approach worked out by Zonneveld (1992).

We also note that the spatial structure of asynchrony will itself affect the (dis)advantages of dispersal. Here, the asynchrony function was the same everywhere in the patch, but among patches within a landscape or along environmental gradients, the temporal distribution of reproductive activity may be centered or shaped differently. If neighboring individuals tend to emerge at the same time, dispersal may be mostly detrimental. On the other hand, individuals on the tail of the distribution might actually increase their mating opportunities if they disperse and seek mates in another spatial location where their timing is more common.

To our knowledge, the interplay between population size, reproductive asynchrony, and evolutionary change has not been examined in a spatial context and would be an exciting next step. Previous studies have established that asynchrony can be strongly selected for as an effective

bet-hedging strategy in the face of environmental unpredictability in high-density populations (Iwasa 1991; Iwasa and Levin 1995). However, when population size is also considered, a tension arises as to whether selection can act quickly enough to alter reproductive asynchrony (or associated mating behaviors) before the population declines to extinction. Gascoigne et al. (2009) discuss traits that could be subject to evolutionary change in the context of mate-finding Allee effects, several of which are relevant to spatial reproductive dynamics.

Overall, a key lesson emerging from this work is that the timing of population dynamic processes can have major consequences for the ability of populations to persist in finite habitat patches. Roland et al. (2000) demonstrated that population density plays a strong role in determining the extent to which butterflies are willing to emigrate from a patch, with emigration being much higher from low-density patches. Reproductive asynchrony, which is common in diverse species and can actually be strongly selected for in many environments (e.g., Post et al. 2001; Satake et al. 2001), exacerbates this link between population density and edge permeability because the extent of asynchrony in a population sets the effective density of that population. Effective density, which reflects the density as perceived by individuals in a population (Kokko and Ebenhard 1996), may be far more important to movement behavior or decision making more generally than is density per se. Structured population models, which allow ecologists to partition individuals into demographic stages or other categories, often improve our understanding of density-dependent dynamics (Murdoch 1994; Turchin 2003). Similarly, asynchrony models that keep track of the extent to which individuals may overlap with each other in time may afford unique insights into dynamics that depend on effective density, including cases such as the present model, where the joint consideration of asynchrony and spatial dynamics has important consequences for population persistence in fragmented landscapes.

Acknowledgments

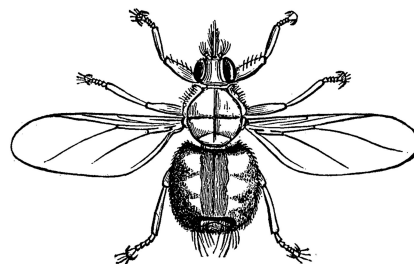
We thank C. Che-Castaldo, E. Goldberg, H. Lynch, and L. Ries and for comments that improved the manuscript. W.F.F. was supported by National Science Foundation (NSF) grant DEB-0624163. C.C. was partially supported by NSF grants DMS-0514839 and DMS-0816068. J.M.C. was supported by the European Union PATtern RESilience (PATRES) project (NEST 43268). High-performance computing facilities at the National Center for Ecological Analysis and Synthesis and the University of Maryland facilitated the numerical analyses presented here.

Literature Cited

- Augsburger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775–788.
- Barrows, E. M. 1975. Mating behavior in halictine bees (Hymenoptera: Halictidae): copulatory behavior and olfactory communication. *Insectes Sociaux* 22:307–331.
- Berwaerts, K., P. Aerts, and H. Van Dyck. 2006. On the sex-specific mechanisms of butterfly flight: flight performance relative to flight morphology, wing kinematics, and sex in *Pararge aegeria*. *Biological Journal of the Linnean Society* 89:675–687.
- Boukal, D. S., and L. Berec. 2002. Single-species models of the Allee effect: extinction boundaries, sex ratios, and mate encounters. *Journal of Theoretical Biology* 218:375–394.
- Bullock, S. H., and K. S. Bawa. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. *Ecology* 62:1494–1504.
- Calabrese, J. M., and W. F. Fagan. 2004. Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *American Naturalist* 164:25–37.
- Calabrese, J. M., L. Ries, S. F. Matter, J. Auckland, J. Roland, D. M. Debinski, and W. F. Fagan. 2008. Reproductive asynchrony in natural butterfly populations and its consequences for female matelessness. *Journal of Animal Ecology* 77:746–756.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee effects in ecology and conservation. Oxford University Press, Oxford.
- Crone, E. E., and C. B. Schultz. 2008. Old models explain new observations of butterfly movement at patch edges. *Ecology* 89:2061–2067.
- Dennis, R. L., and T. G. Shreeve. 2008. Hostplant-habitat structure and the evolution of butterfly mate-locating behaviour. *Zoological Journal of the Linnean Society* 94:301–318.
- Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* 153:165–182.
- Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* 51:355–372.
- Gilchrist, G. W. 1990. The consequences of sexual dimorphism in body size for butterfly flight and thermoregulation. *Functional Ecology* 4:475–487.
- Hanski, I., C. Eralahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7:958–966.
- Hopper, K. R., and R. T. Roush. 1993. Mate finding, dispersal, number released, and the success of biological-control introductions. *Ecological Entomology* 18:321–331.
- Hutchinson, J. M. C., and P. M. Waser. 2007. Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews* 82:335–359.
- Iwasa, Y. 1991. Asynchronous pupation of univoltine insects as evolutionary stable phenology. *Researches on Population Ecology* 33: 213–227.
- Iwasa, Y., and S. A. Levin. 1995. The timing of life-history events. *Journal of Theoretical Biology* 172:33–42.
- Kemp, D. J., C. Wiklund, and K. Gotthard. 2006. Life history effects upon contest behaviour: age as a predictor of territorial contest dynamics in two populations of the speckled wood butterfly, *Pararge aegeria* L. *Ethology* 112:471–477.

- Kokko, H., and T. Ebenhard. 1996. Measuring the strength of demographic stochasticity. *Journal of Theoretical Biology* 183:169–178.
- Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:319–334.
- Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* 82:384–392.
- Labine, P. A. 1964. Population biology of the butterfly, *Euphydryas editha*. I. Barriers to multiple inseminations. *Evolution* 18:335–336.
- Landolt, P. J., and T. W. Phillips. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annual Review of Entomology* 42:371–391.
- Manly, B. F. J. 1974. Estimation of stage-specific survival rates and other parameters for insect populations developing through several stages. *Oecologia (Berlin)* 15:277–285.
- McCarthy, M. A. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling* 103:99–102.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Ovaskainen, O., M. Luoto, I. Ikonen, H. Rekola, E. Meyke, and M. Kuussaari. 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist* 171:610–619.
- Post, E., S. A. Levin, Y. Iwasa, and N. C. Stenseth. 2001. Reproductive asynchrony increases with environmental disturbance. *Evolution* 55:830–834.
- Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491–522.
- Robinet, C., D. R. Lance, K. W. Thorpe, K. S. Onufrieva, P. C. Tobin, and A. M. Liebhold. 2008. Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *Journal of Animal Ecology* 77:966–973.
- Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81:1642–1653.
- Rutowski, R. L., L. McCoy, and M. J. Demlong. 2001. Visual mate detection in a territorial male butterfly (*Asterocampa leilia*): effects of distance and perch location. *Behaviour* 138:31–43.
- Satake, A., A. Sasaki, and Y. Iwasa. 2001. Variable timing of reproduction in unpredictable environments: adaptation of flood plain plants. *Theoretical Population Biology* 60:1–15.
- Schiestl, F. P., and M. Ayasse. 2000. Post mating odor in females of the solitary bee, *Andrena nigroaenea* (Apoidea, Andrenidae), inhibits male mating behavior. *Behavioral Ecology and Sociobiology* 48:303–307.
- Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, NJ.
- Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *American Naturalist* 148:255–274.
- Waldbauer, G. P. 1978. Phenological adaptation and polymodal emergence patterns of insects. Pages 127–144 in H. Dingle, ed. *Evolution of insect migration and diapause*. Springer, New York.
- Wells, H., P. H. Wells, and P. Cook. 1990. The importance of overwinter aggregation for reproductive success of monarch butterflies (*Danaus plexippus* L.). *Journal of Theoretical Biology* 147:115–131.
- Wickman, P. O. 1992. Sexual selection and butterfly design: a comparative study. *Evolution* 46:1525–1536.
- Wiklund, C., and T. Fagerström. 1977. Why do males emerge before females? a hypothesis to explain the incidence of protandry in butterflies. *Oecologia (Berlin)* 31:153–158.
- Wiklund, C., K. Gotthard, and S. Nylin. 2003. Mating system and the evolution of sex-specific mortality rates in two nymphalid butterflies. *Proceedings of the Royal Society B: Biological Sciences* 270:1823–1828.
- Yamanaka, T., and A. M. Liebhold. 2009. Spatially implicit approaches to understand the manipulation of mating success for insect invasion management. *Population Ecology* 51:427–444.
- Zonneveld, C. 1992. Polyandry and protandry in butterflies. *Bulletin of Mathematical Biology* 54:957–976.
- Zonneveld, C., and J. A. J. Metz. 1991. Models on butterfly protandry: virgin females are at risk to die. *Theoretical Population Biology* 40:308–321.

Associate Editor: Thomas N. Sherratt
Editor: Mark A. McPeck



“We figure, from a specimen in the Museum of the Peabody Academy, the Bird-tick, *Ornithomyia*, which lives upon the Great Horned Owl. Its body is much flattened, adapted for its life under the feathers, where it gorges itself with the blood of its host.” From “A Chapter on Flies (Concluded)” by A. S. Packard Jr. (*American Naturalist*, 1869, 2:638–644).