

How protandry and protogyny affect female mating failure: a spatial population model

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Abstract

Population growth and persistence depend on the collective ability of individuals to find mates in both space and time. When individuals are reproductively mature for only a portion of a population's breeding season, reproductive asynchrony can cause mating failure and a temporal Allee effect, which is exacerbated by spatial constraints in isolated populations. However, the effect of phenological variation by sex (protandry, protogyny) in spatiotemporal mate finding is not well understood. Here, we examine the interacting roles of sex-specific and population-wide individual asynchrony on female matelessness in spatially isolated populations. By incorporating sex-specific phenology into a two-sex reaction-diffusion system, we explore female matelessness as a function of phenology, movement behavior, and patch size. Although individual asynchrony may lead to female mating failure in small and isolated populations, we find that moderate protandry reduces female mating failure across a variety of scenarios. We go on to examine model behavior for a case study based on the bagworm, *Thyridopteryx ephemeraeformis* Haworth (Lepidoptera: Psychidae), where many populations exhibit pronounced protogyny. Overall, we find a consistent benefit of moderate protandry, which may mitigate female matelessness for many populations.

Introduction

Population persistence and growth are dependent on the ability of individuals to find mates. Mate finding is of particular concern for species with low-density populations because difficulties in finding mates in space and time can lead to decreased per capita population growth (component Allee effect; Stephens & Sutherland, 1999). In empirical systems, difficulties in mate finding have been explored primarily in the context of space (Hissmann, 1990; Groom, 1998; Tsuda & Miller, 1998), attending to both mate-finding behaviors (Eggert, 1992; Ruther et al., 2000; Schiestl & Ayasse, 2000) and mate-finding Allee effects (McCarthy, 1997; Gascoigne et al.,

2009). Temporal aspects of mate finding have been considered at the level of the individual (Gowaty & Hubbell, 2009), but rarely have population-level effects been addressed. Although often neglected in ecological studies, the temporal aspect of mate finding has equally important consequences for many populations with discrete breeding periods or reproductive asynchrony (see Calabrese & Fagan, 2004; Calabrese et al., 2008; Robinet et al., 2008; Fagan et al., 2010; Rhainds & Fagan, 2010).

Reproductive asynchrony may isolate individuals from potential mates. At the population level, reproductive asynchrony arises through a combination of variation in individual phenology and sex-specific phenology. Reproductive asynchrony through individual phenological variation is a bet-hedging strategy employed by many insect and plant species in unpredictable environments (Hopper, 1999). However, in small populations, this same form of reproductive asynchrony can lead to female matelessness and be a mechanism for the Allee effect (Calabrese &

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Fagan, 2004). Reproductive asynchrony also occurs through sex-specific phenology. Protandry, in which males are reproductively active before females, appears common (Honek, 1997; Morbey & Ydenberg, 2001), but examples of protogyny, in which females become reproductively active first, are also known (Honek, 1997; Buck, 2001). Protandry has been studied extensively and can be an evolutionarily stable strategy that increases both male and female reproductive success (Wiklund & Fagerström, 1977; Zonneveld & Metz, 1991; Carvalho et al., 1998; del Castillo & Nunez-Farfan 2002): however, the amount of protandry that maximizes reproductive success for an individual may differ between males and females (Zonneveld & Metz, 1991). Furthermore, excessive protandry can exacerbate the negative effects of reproductive asynchrony and lead to substantial female mating failure (Calabrese & Fagan, 2004; Calabrese et al., 2008). Overall, the interactions between sex-specific phenology, individual asynchrony, and spatial mate-finding processes on female mating success in small populations are not well understood. In addition, the links between spatiotemporal components of reproductive asynchrony and mate-finding behavioral adaptations have rarely been explored (Fagan et al., 2010). For example, the ability of males to discriminate between previously mated and virgin females is widespread in insects (Friberg, 2006; Thomas, 2011), but it remains unclear whether this behavior has an impact on the mating success of females at low population density. In the case of insect species with flightless females, the role of male dispersal on the local mating success of females has rarely been investigated (Rhainds, 2012).

Here, we build upon an established spatially explicit model of reproductive asynchrony (Fagan et al., 2010) to address population-level effects of sex-specific phenology. Previous work using this model has shown that individual asynchrony may increase the proportion of females that die unmated in isolated populations, and that female matelessness is exacerbated by high rates of diffusive dispersal (Fagan et al., 2010). Using numerical solutions, we calculate the expected fraction of mateless females as a function of individual and sex-specific reproductive asynchrony and patch size. Going beyond purely random movement, we also consider how more realistic directed movements, in which males actively seek out females, modulate the combined effects of asynchrony and protandry/protogyny on female matelessness.

The model is developed using the bagworm *Thyridopteryx ephemeraeformis* Haworth (Lepidoptera: Psychidae) as a case study. Recent work has found that mating failure contributes to setting the northern range limit of the bagworm (Rhainds & Fagan, 2010; Rhainds, 2012). Northern (range-margin) populations of the bagworm experience

both individual asynchrony and sex-specific variation in phenology which lower effective population density, leading to substantial – in some cases, total – female mating failure (Rhainds & Fagan, 2010). Interestingly, a remarkable diversity of emergence patterns has been observed in bagworm populations, including both protandry and protogyny. The neotenic female bagworms attract males for mating by releasing pheromone-impregnated setae into the lower segment of the bag it constructed as a larva (Leonhardt et al., 1983). Because the release of pheromone from the setae is potentially independent from the female mating status, it remains unclear whether males are capable of discriminating between mated and virgin females (Rhainds et al., 1994). Therefore, to complement our theoretical modeling, we also explore the consequences of protandry/protogyny on bagworm reproductive success using field data from range-margin and range-interior populations as case studies.

Materials and methods

Basic reproductive timing model

As described by Calabrese et al. (2008), any basic model of reproductive asynchrony must incorporate (1) individual-level reproductive activity periods that are only a fraction of the population-level breeding period, (2) females that may die unmated, and (3) explicit population densities of males and females throughout the population-level breeding period. Building on earlier work by Manly (1974), Zonneveld & Metz (1991) developed a model of emergence and death that was later used to explore population-level consequences of individual and sex-specific phenology (e.g., Zonneveld & Metz, 1991; Calabrese et al., 2008):

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

$$\frac{dF}{dT} = F_0 g(t - \tau, \theta_f) - \alpha F, \quad (1b)$$

where t is time in days, M_0 and F_0 are total densities of males and females, respectively, $g(t, \theta)$ is the probability distribution (with parameter vector θ) that governs reproductive timing, τ (which takes positive values for protandry and negative values for protogyny) determines the sex-specific temporal shift in reproductive activity, and α is a constant, per-day death rate. The subscripts m and f allow the model parameters to differ between males and females. As in previous work (Calabrese et al., 2008; Fagan et al., 2010), the onset of reproductive activity (which we term ‘emergence’) is modeled using the gamma probability density function:

$$g(t, \theta) = \frac{\lambda}{\Gamma(\mu)} (\lambda t)^{\mu-1} e^{-\lambda t}, \quad (2)$$

for $t \geq 0$, where $\theta = (\lambda, \mu)$, λ is the inverse scale parameter, μ is the shape parameter, and $\Gamma(\mu)$ is the gamma function. The gamma distribution is a good choice here because it is flexible in shape, has a bounded left tail that provides a defined ‘start point’ to the population’s reproductive period, and is relatively parameter sparse. To model general sex-specific phenological variation in the population, we hold the shape of the gamma distributions constant across the sexes ($\theta_m = \theta_f$), but modify τ to shift the male distribution relative to the female distribution (Figure 1). We also consider alternative, biologically realistic emergence patterns in a scenario incorporating empirically determined θ_m and θ_f from populations of bagworm. The model assumes non-overlapping generations and no net immigration or emigration, and examines the population density of males and females throughout a breeding period of length T .

To examine the proportion of females in the population that goes mateless during the breeding season, this model is expanded by incorporating a mating function and tracking mated and unmated females separately. We apply the standard kinetic approach to mate encounter, which assumes that mating frequency is proportional to the densities of males and unmated females at any given time. Unmated females (U) are modeled using the following equation:

$$\frac{dU}{dt} = F_0 g(t - \tau, \theta_f) - c(\cdot)MU - \alpha U, \quad (3)$$

where c represents the instantaneous mating efficiency, which we assume to be constant at $c = 0.1$, drawing on

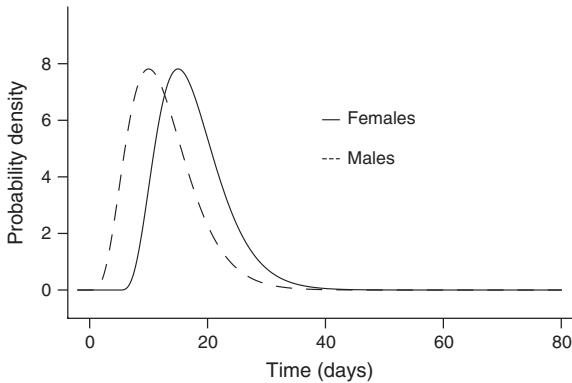


Figure 1 Gamma probability distribution of adult emergence with individual asynchrony ($\theta_m = \theta_f = 0.4$) and sex-specific phenology (5 days protandry; $\tau = 5$).

results from Calabrese et al. (2008). One mating is assumed sufficient for successful reproduction, and no additional benefit of multiple matings is considered. The accumulated density of mated females is found by solving:

$$\frac{dR}{dt} = c(\cdot)MU. \quad (4)$$

Spatial model

A spatial model of the above system was developed in Fagan et al. (2010), which includes further description of the model and solution via a Fourier approximation. We incorporate one-dimensional explicit space into the above system to model an insect population within a discrete habitat patch. In the spatial model, males and females move according to the same diffusion process. However, mate-finding behaviors in many insects include attraction toward prospective mates, via pheromones or other cues. We therefore incorporate the additional potential for advective movement toward females by males. Mated females are assumed to lay all eggs inside the patch, contributing to the next generation of the population. The spatial model for a patch of size L is as follows:

$$\frac{dM}{dt} = M_0 g(t - \tau, \theta_m) - \alpha M + D \frac{\partial^2 M}{\partial x^2} + B_A \frac{\partial}{\partial x} M \frac{\partial A}{\partial x}, \quad (5)$$

$$\frac{dF}{dt} = F_0 g(t - \tau, \theta_f) - \alpha F + D \frac{\partial^2 F}{\partial x^2},$$

$$\frac{dU}{dt} = F_0 g(t - \tau, \theta_f) - c(\cdot)MU - \alpha U + D \frac{\partial^2 U}{\partial x^2}, \text{ and}$$

$$\frac{dR}{dt} = c(\cdot)MU,$$

with diffusion coefficient D and advection coefficient B_A . In a scenario in which $A = F$, males are attracted to all females and advect up a spatial gradient of female density; conversely, when $A = U$, males discriminate between mated and unmated females, and move specifically toward areas with higher densities of unmated females. Here, we assume a balanced sex ratio where $M_0 = F_0 = 100$ and death rate $\alpha = 0.2$.

We consider two alternate behaviors at the patch edge. Initially, we assume that animals exhibit no change in movement behavior when encountering the patch edge and that any emigration from the patch is a loss to the local population. This leads to a scenario in which patch edges are given by Dirichlet (absorbing) boundary conditions:

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

However, this is not a biologically realistic scenario for many species, which may actively avoid edges between preferred and other habitat types (Ross et al., 2005). Therefore, we also consider the alternative scenario in which individuals stay exclusively within the patch and there is no loss to the local population from emigration. In t case, patch edges are given reflecting boundary conditions:

$$\begin{aligned} \frac{\partial}{\partial x} M(t, 0) = \frac{\partial}{\partial x} M(t, L) = \frac{\partial}{\partial x} F(t, 0) = \frac{\partial}{\partial x} F(t, L) = \\ \frac{\partial}{\partial x} U(t, 0) = \frac{\partial}{\partial x} U(t, L) = \frac{\partial}{\partial x} R(t, 0) = \frac{\partial}{\partial x} R(t, L) = 0. \end{aligned} \quad (7)$$

In both cases, the population densities at time $t = 0$ are 0:

$$M(0, x) = F(0, x) = U(0, x) = R(0, x) = 0. \quad (8)$$

The total proportion of females that dies mateless in a patch of size L can be calculated as:

$$q^* = 1 - \frac{\int_{x=0}^{x=L} R(T, x) dx}{F_0 L}. \quad (9)$$

To assess the population consequences of female matelessness, we assume geometric growth of the population across breeding seasons:

$$N_{t+1} = \delta N_t (1 - q^*), \quad (10)$$

where female population density N increases by a finite rate of increase δ when all females are mated. To quantify the consequences of female matelessness under different scenarios of individual asynchrony, sex-specific phenology, movement behaviors and patch size, we calculate the minimum geometric growth rate that will allow population persistence, δ^* :

$$\delta^* = \frac{-1}{q^* - 1} = \frac{F_0 L}{\int_{x=0}^{x=L} R(T, x) dx}. \quad (11)$$

The above system of partial differential equations was solved numerically using the function `NDSolve[]` in MATHEMATICA version 6.0 (Wolfram Research, Champaign, IL, USA).

We also consider alternative, biologically realistic emergence patterns based on field observations of the bagworm. Populations of bagworm exhibit a range of emergence patterns across the species' geographic range. Here, we incorporate empirically determined θ_m and θ_f for range-interior and range-margin populations of the

bagworm. These emergence parameters were calculated using repeated field surveys conducted by one of us (MR). These monitoring data were aggregated by latitude to produce a cumulative distribution function (CDF) of adult emergence for males and females; the emergence parameters we use are based on the maximum likelihood fit of the gamma distribution to the CDF (HL Lynch, M Rhainds, JM Calabrese, S Cantrell, C Cosner & WF Fagan, unpubl.). We contrast biologically realistic emergence patterns from three latitudinal ranges: (1) range-interior (southern) populations in the 38.75–39.00°N latitude, which exhibit ca. 0.8 days protogyny and relatively low individual-level asynchrony, (2) range-interior (southern) populations from 39.00 to 39.25°N latitude, which exhibit ca. 0.7 days protandry and relatively low individual-level asynchrony, and (3) range-margin (northern) population of the bagworm from 41.50 to 41.75°N latitude, which exhibit ca. 5.9 days protogyny and relatively high individual-level asynchrony. We use these emergence patterns from the bagworm to test the relevance of our model for natural populations.

Results

The geometric population growth rate (δ^*) necessary to offset cumulative female matelessness (q^*) for a given population arises from the interplay between phenology and dispersal-mediated loss across the patch edge. In our results, we plot δ^* as a series of contours that demonstrate the benefits and costs of asynchrony in an isolated population. With this presentation, we can also determine the critical patch size for population persistence for a given δ^* .

In the absence of dispersal, δ^* is not affected by patch size, but depends only on temporal isolation via asynchrony, whether due to individual variation (Figure 2A), sex-specific phenology (Figure 2B), or some combination thereof (Figure 2C and D). When phenology is affected by both sex-specific emergence and individual asynchrony, the relative effect of each factor on mate-finding success depends on the relative magnitude of the phenological changes. In populations in which there is little individual variation in phenology that is not sex specific (i.e., populations with high λ), sex-specific phenology is the main driver of mate-finding success or failure in the population, and populations with even slight protogyny can experience substantial female matelessness due to the temporal separation of males and females (Figure 2). Modest protandry (i.e., males ahead by 1–3 days) is the optimal condition for the scenarios considered, and this mitigates the loss of mating opportunities arising from moderate individual-level variation in phenology. However, protandry is unable to buffer the population from the loss of female reproduc-

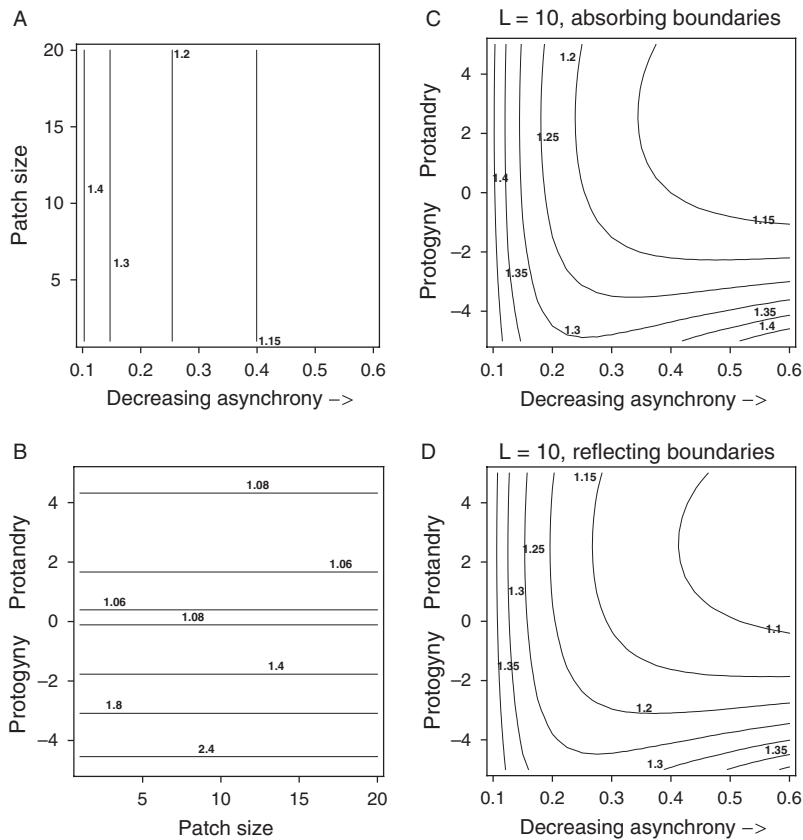


Figure 2 Contours of geometric population growth rate δ^* necessary for population persistence as function of the degree of individual asynchrony (λ), protandry/protogyny (τ), and patch size L in the absence of dispersal. (A) No sex-specific variation in phenology: δ^* depends only on the degree of individual-level asynchrony in the population. (B) No individual-level variation in phenology: δ^* depends only on the degree of protandry/protogyny in the population, and the minimum δ^* occurs around 1 day protandry. (C) Patch size $L = 10$, and δ^* varies with both sex-specific and individual-level variation in the population. (D) The same δ^* contours as panel C when reflecting boundaries are used. Parameters are $c = 0.1$, $\mu = 5$, $\alpha = 0.2$, and $M_0 = F_0 = 100$.

tive capacity when individual-level asynchrony is high (low λ). By adding loss across the patch boundary as another mechanism by which unmated females may exit the population, dispersal via simple diffusion dramatically increases female matelessness and raises the reproductive cost of both protogyny and individual-level asynchrony in isolated populations (Figure 3). As the diffusion rate increases, the value of δ^* necessary for population persistence with any given pattern of asynchrony also increases (Figure 3A and B).

Male attraction toward females may exacerbate or mitigate female matelessness, depending on the context (Figure 4). Attraction to any female exacerbated female mating failure except in the smallest patches (Figure 4D), whereas attraction toward unmated females always increased the proportion of females who mated (Figure 4B). Interestingly, the addition of male attraction to females (either indiscriminate or selective) does not change the optimal conditions for sex-specific phenology: moderate protandry (of 1–3 days in these scenarios) remains optimal irrespective of the movement scenarios we considered. In small habitat patches, the benefit of selective attraction is strongest for both protandrous and

protogynous populations, but in larger patches male advection toward unmated females is more beneficial in protandrous populations.

In our model of bagworm phenology, the populations demonstrate a range of sex specific (protogyny and protandry) and individual-level variation in phenology (Figure 5); individual variation is higher for the range-margin population. The population growth rate necessary for population persistence is consistently largest for range-margin populations, which exhibit the highest protogyny and the highest individual-level asynchrony. The necessary population growth rate is smallest for protogynous range-interior populations, which exhibit the lowest level of individual variation. In protandrous range-interior populations, the existing sex-specific phenology is optimal under all movement conditions considered. In protogynous range-interior populations, the levels of protogyny observed for bagworms necessitate a 2% larger population growth rate than would be necessary for a protandrous population with the same level of individual asynchrony in the absence of any movement dynamics (at $L = 20$; Figure 6). Conversely, given the differences in individ-

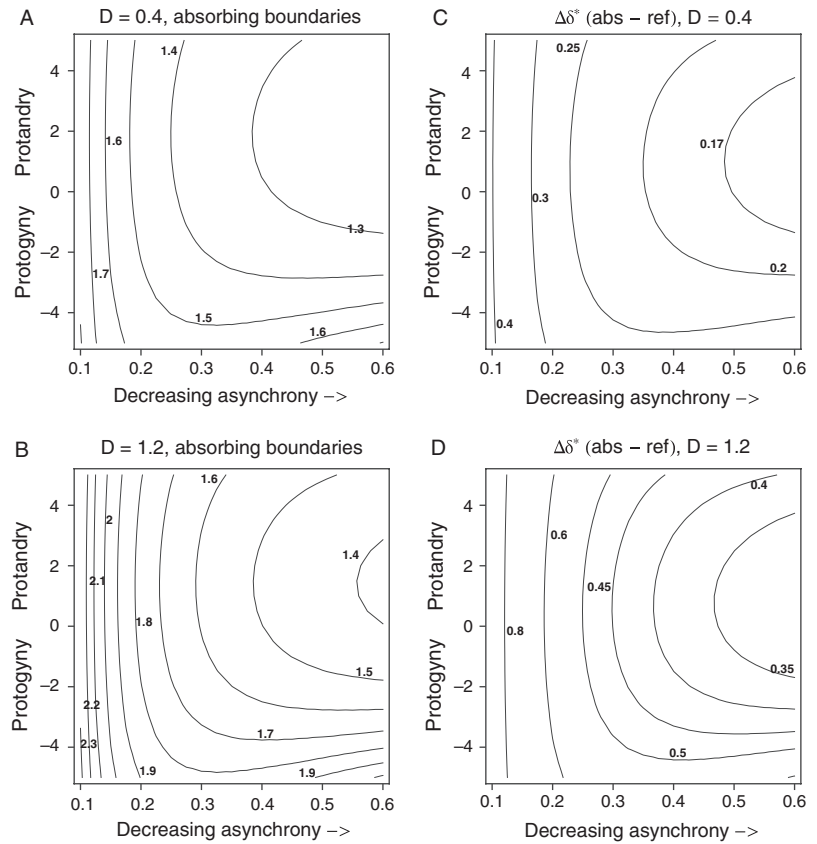


Figure 3 Contours of geometric population growth rate δ^* necessary for population persistence as function of individual-level asynchrony and protandry/protogyny for contrasting pairs of simple diffusion and edge dynamics. Panels (A) and (B) show δ^* contours when dispersal can lead to loss via emigration from the patch (patches have absorbing boundaries), at low and high diffusive dispersal. Panels (C) and (D) plot the difference in critical population growth rate ($\Delta\delta^*$, calculated as $\delta^*_{\text{abs}} - \delta^*_{\text{ref}}$) for populations with and without emigration. Parameters are $c = 0.1$, $\mu = 5$, $\alpha = 0.2$, $M_0 = F_0 = 100$, $L = 10$, and $B_A = 0$.

ual asynchrony, protandrous range-interior populations require a 10% larger population growth rate than range-interior protogynous populations (at $L = 20$) without movement dynamics (Figure 6A and D). When diffusion and advection are accounted for, this requirement increases to 31% (at $L = 20$, $B_F = 1$), or as high as 56% in small patches ($L = 10$, $B_F = 1$; Figure 6C and F). Scenarios where males distinguish between mated and unmated females result in less female mating failure in range-interior protogynous populations and in all but the smallest patches for protandrous populations. However, in range-margin populations, there is so much individual variation in phenology that sex-specific phenology has little additional impact on female mating failure (Figure 6C) and male attraction to all females is more beneficial than attraction to unmated females. Most notably, the population growth rate necessary for persistence of range-margin populations is over twice that needed by range-interior protogynous populations under the same conditions (Figure 6C and I). Overall, the results of these bagworm models confirm that moderate protandry and

low levels of individual asynchrony may improve female mating success across the explored scenarios.

Discussion

We have applied a theoretical modeling framework that unified the spatial and temporal components of mate-finding behavior to examine the interaction of sex specific and individual-level asynchrony as they relate to mate finding for isolated populations. Independently, individual asynchrony and sex-specific phenology both influence the temporal dynamics of mate finding. Both types of phenological variation have the potential to decrease reproductive success due to temporal isolation, which is exacerbated by emigration from small patches via dispersal. When phenological variation inhibits female mate finding (Figure 2), a higher population growth rate is necessary to offset the loss of reproductive potential. The relative importance of sex-specific phenological variation and individual-level asynchrony varies depending on which of those two factors is the dominant controller of the overlap between potential mates. When individual

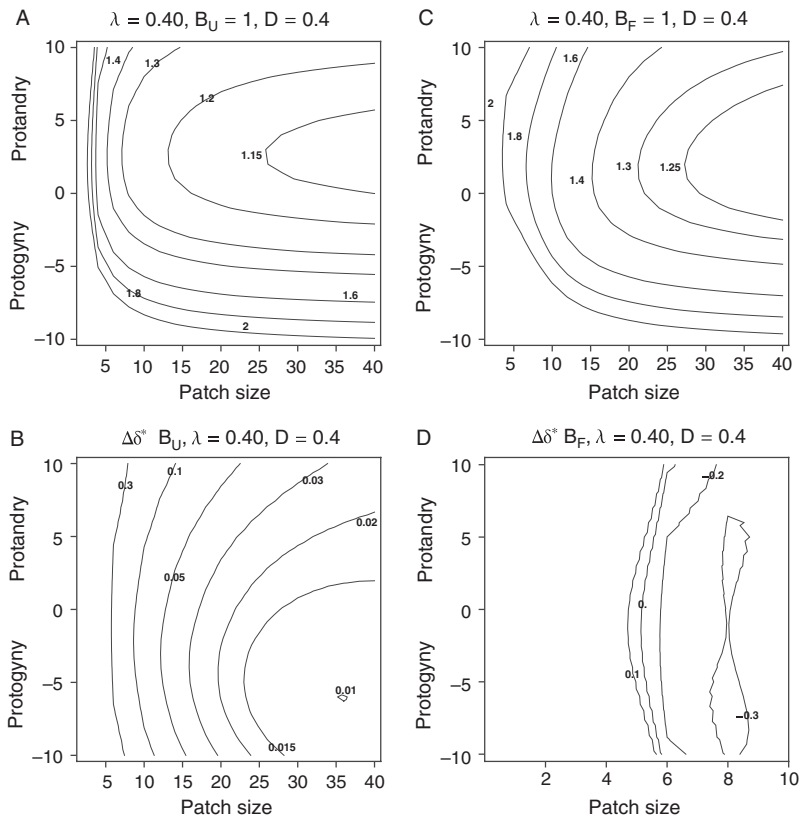


Figure 4 Contours of the critical population growth rate δ^* necessary for population persistence as function of individual-level asynchrony and protandry/protogyny for contrasting male movement behaviors at different rates of diffusive dispersal. Panel (A) shows δ^* contours when males are attracted to unmated females ($B_U = 1$; patches have absorbing boundaries). Panel (C) shows δ^* contours when males are attracted to all females ($B_F = 1$; patches have absorbing boundaries). Panels (B) and (D) plot the difference $\Delta\delta^*$ in the critical population growth rate between scenarios with diffusion only and diffusion plus advection, calculated as $\delta^*_{D} - \delta^*_{D+B}$. However, note the change in x-axis for panel (D), to better show the $\Delta\delta^*$ contours distinguishing when attraction to all females is harmful vs. beneficial. Panel (B) demonstrates that male advection toward unmated females is most beneficial in highly asynchronous or protandrous populations, whereas panel (D) demonstrates that indiscriminate advection toward females is most detrimental in small patches, but becomes very slightly advantageous in the smallest patches ($L < 5$ in our scenarios). Parameters are $c = 0.1$, $\mu = 5$, $\alpha = 0.2$, $M_0 = F_0 = 100$, $L = 10$, and absorbing boundary conditions.

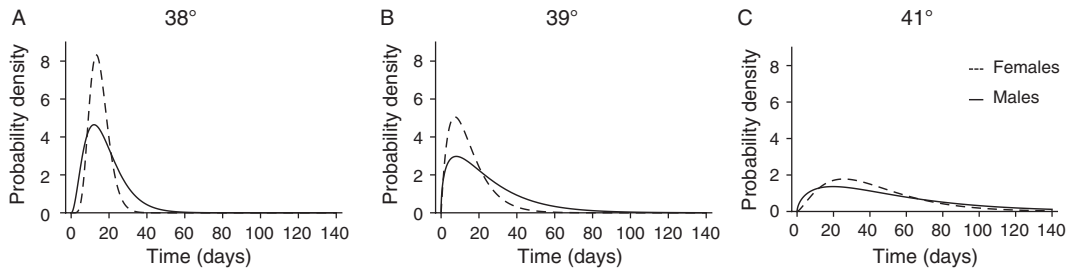


Figure 5 Sex-specific emergence patterns of bagworms for application of the model to range-interior and range-margin bagworm populations. Emergence distributions of bagworms at (A) 38.75–39.00°N (‘38°’), (B) at 39.00–39.25°N (‘39°’), and (C) at 41.50–41.75°N (‘41°’). Gamma distribution parameters are taken from HL Lynch, M Rhainds, JM Calabrese, S Cantrell, C Cosner & WF Fagan (unpubl.).

variation is very high, any effect of protandry or protogyny is swamped out, and sex-specific variation in phenology

confers no mate-finding benefits or costs to the population. This is consistent with the results found in an

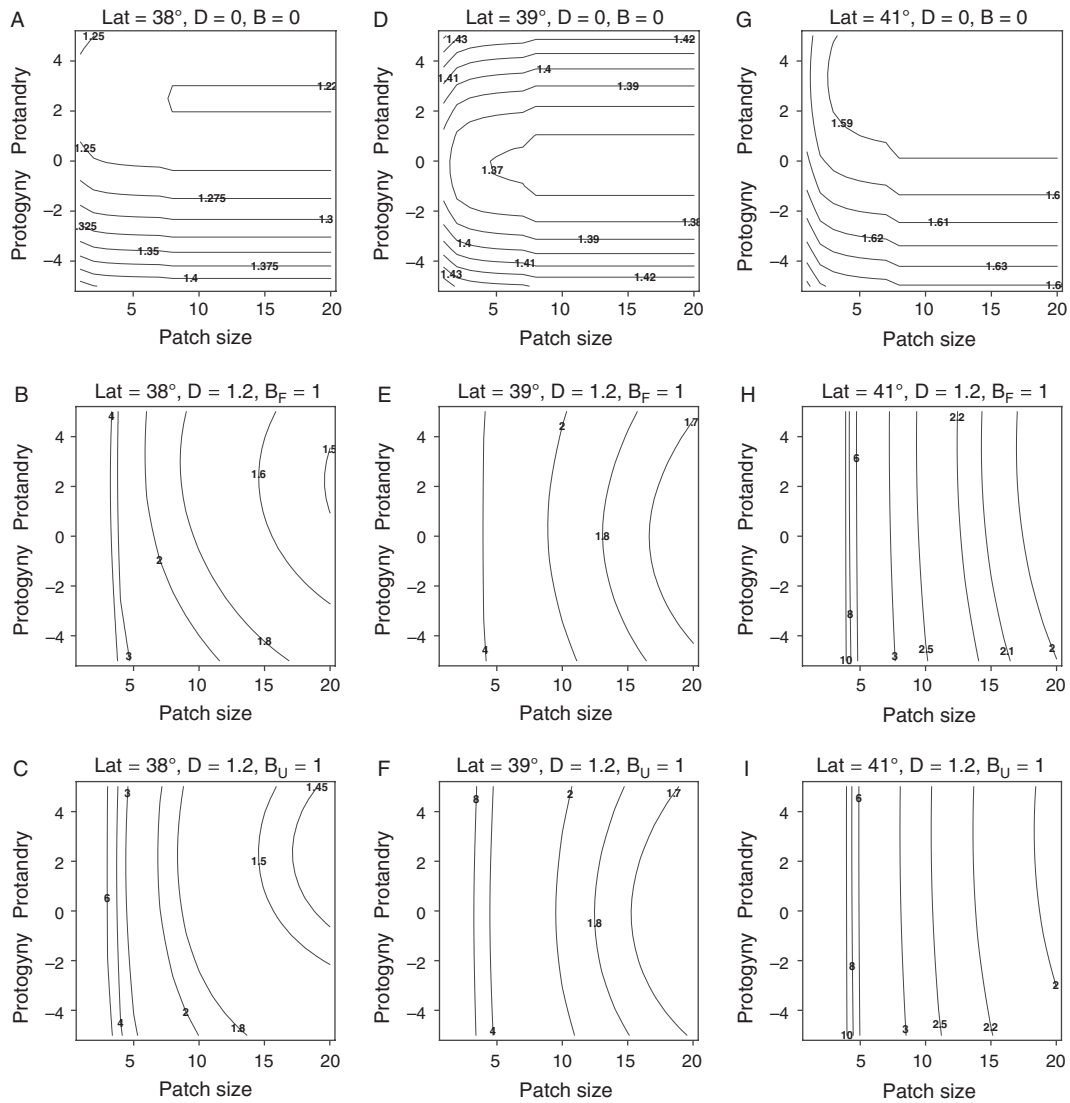


Figure 6 Application of the model to range-interior and range-margin bagworm populations. Panels show the contours of geometric population growth rate δ^* necessary for population persistence as function of additional protandry/protogyny (the existing sex-specific phenology for each population occurs at $y = 0$ in all panels) and patch size for each population. (A–C) Results based on emergence distributions of bagworms at 38.75–39.00°N (‘Lat = 38°’), (D–F) at 39.00–39.25°N (‘Lat = 39°’), and (G–I) at 41.50–41.75°N (‘Lat = 41°’). Panels (A), (D), and (G) show δ^* contours in the absence of any movement ($D = 0$, $B = 0$), panels (B), (E), and (H) incorporate diffusive dispersal and indiscriminate attraction to females ($D = 1.2$, $B_F = 1$), and panels (C), (F), and (I) incorporate diffusive dispersal and attraction toward unmated females ($D = 1.2$, $B_U = 1$). Parameters for all panels are $c = 0.1$, $\alpha = 0.2$, $M_0 = F_0 = 100$, and absorbing boundary conditions.

individual-based model by Calabrese & Fagan (2004), in which 2 days protandry did not make a difference in the dynamics of populations that were already highly asynchronous at the individual level. Overall, we found individual-level asynchrony to increase female matelessness in a population, a result that is consistent with previous studies (e.g., Calabrese & Fagan, 2004; Calabrese et al., 2008; Robinet et al., 2008; Fagan et al., 2010).

In contrast, in populations with low levels of individual-level asynchrony, sex-specific phenological variation can have substantial consequences for female mating success. Specifically, protandry tends to decrease (and protogyny tends to increase) female mating failure. In our spatial model, effective population growth rate is maximized with modest amounts of protandry, a result that parallels findings in the non-spatial models of Wiklund & Fagerström

(1977), Zonneveld & Metz (1991), and Kleckner et al. (1995) where protandry conferred a fitness benefit on individuals. Our results add to these findings, confirming that some protandry is beneficial across a range of movement scenarios. However, after accounting for the additional mating failures arising from dispersal-mediated loss across the patch boundary, extreme protandry (more than a few days) may again increase female matelessness, such that a modest degree of protandry becomes optimal. Moderate protandry consistently led to low female matelessness across the range of spatial scenarios we considered. The benefits of protandry were accentuated in large habitat patches and in populations with low levels of individual asynchrony. Overall, protandry appears to confer benefits to individual fitness (i.e., higher probabilities of successful mating) regardless of patch size and boundary conditions, potentially mitigating matelessness due to individual-level asynchrony. This result was robust to changes in movement strategies and edge dynamics that contribute to spatial losses in a population.

When males are able to distinguish unmated females from mated females, attraction reduces female matelessness and the population growth rate necessary for population persistence, and there is a net benefit to the population (Fagan et al., 2010). Selective male advection mitigates the potential loss of mating opportunities most effectively in populations exhibiting both individual asynchrony and protandry, indicating another potential benefit of protandry in mate finding. This result emphasizes the importance of considering both spatial and temporal components of mate finding, underscoring the limitations of our understanding of the cues used in insect populations to identify potential mates. Although many studies have identified pheromonal or other cues male insects use to locate females, limited work has identified cues to mating status of potential mates (Eggert, 1992; Ruther et al., 2000). Some evidence shows that pheromonal cues and behavior mechanisms may both be used in some insect populations to differentiate the mating status of potential mates (Labine, 1964; Fauvergue et al., 1995; Schiestl & Ayasse, 2000; Thomas, 2011). Our work suggests that more detailed study is needed to determine whether cues used for locating potential mates in fact convey mating status information as well as locational information to searching males.

In considering more biologically realistic emergence patterns for incorporating sex-specific phenology into our model scenarios, we found that the high degree of individual-level asynchrony present in range-margin bagworm populations generally swamped the effect of protandry/protogyny on female mating failure. Under the conditions of our model, range-interior populations with

low individual-level asynchrony and slight protogyny fared best, whereas the high levels of protogyny and individual-level asynchrony in range-margin populations aggravated female matelessness under all the scenarios we explored. However, additional protandry would minimize female matelessness for range-interior protogynous populations, according to our model. These scenarios again show a benefit of protandry when individual-level asynchrony is low enough.

In the case study of bagworms, the effect of male attraction to females on female mating rate was context dependent, where attraction to all females mitigated female matelessness in more asynchronous populations and small patches, whereas attraction to unmated females led to the lowest female mating failure except in situations with low effective densities and high dispersal-mediated loss of females. This demonstrates the importance of understanding context in assessing the benefits of mate-finding behaviors. Like individual asynchrony, mate-finding behaviors that increase individual fitness in some environments may increase mating failure in others. In bagworms, there is potential for males to be attracted to mated females because the dissemination of pheromone scales is independent of the female mating status (Rhainds et al., 1994); however, how these scales degrade over time and the other cues males may use to distinguish female mating status remain unknown. Although these results cannot be applied to specific bagworm populations – because other model assumptions about movement and mating efficiency do not match bagworm biology (Rhainds & Fagan, 2010; Rhainds, 2012) – they do demonstrate the pertinence of our results for real insect populations with natural phenologies.

Overall, our work indicates the importance of reproductive asynchrony, common in insect populations due to individual-level and sex-specific phenological variation, and the value of moderate protandry for the persistence of small or spatially isolated populations. Both forms of asynchrony may be strongly selected for in a range of environments (e.g., Fagerström & Wiklund, 1982; Post et al., 2001; Satake et al., 2001), but under a variety of scenarios these two factors may act individually or jointly to impact female matelessness and Allee effects in small or isolated populations. Although protandry minimizes female matelessness across a range of scenarios, our results indicate that both protogyny and extreme protandry may exacerbate Allee effects in small populations. Also, the benefits of protandry are limited by the degree of individual-level asynchrony in the population. To build these models, we have simplified both phenology and behavior considerably. However, as we add pieces of biological realism that are potentially important in some species

(e.g., male discrimination of female mating status), we find that the model results sometimes depend on these additional features (Figures 4 and 6). Other factors not considered here may have similar effects on female mating failure and population growth or shrinkage. For example, many scenarios considered here limit sex-specific variation in phenology to a shift in time of a static distribution of emergence, assuming that males and females emerge in the same way even when those emergence patterns begin at different times. However, multiple studies as well as our bagworm case study indicate that the emergence curves for males and females may be dramatically different. Similarly, we assume males and females experience similar mortality, despite evidence to the contrary. Because this system assumes one mating is sufficient for females but allows for males to mate multiple times, we expect that changes to female mortality would affect our model results more significantly than changes to male mortality, and that longer lived females would be less likely to die mateless. We also do not account for the dramatically different dispersal behaviors of the sexes, which are observed in many insect populations including the bagworm because these behaviors vary substantially among species. These simplifications of reality are interrelated as differential mortality rates may be linked to different mating systems or sex-specific dispersal. Future studies can build in one or more of these biological scenarios to explore their respective and interactive impacts on female mating failure.

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