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Lost in Time, Lonely, and Single: Reproductive Asynchrony and the Allee Effect

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ABSTRACT: Identifying linkages between life-history traits and small population processes is essential to effective multispecies conservation. Reproductive asynchrony, which occurs when individuals are reproductively active for only a portion of the population-level breeding period, may provide one such link. Traditionally, reproductive asynchrony has been considered from evolutionary perspectives as an advantageous bet-hedging strategy in temporally unpredictable environments. Here, we explore the dynamic consequences of reproductive asynchrony as a density-dependent life-history trait. To examine how asynchrony affects population growth rate and extinction risk, we used a general model of reproductive timing to quantify the temporal overlap of opposite-sex individuals and to simulate population dynamics over a range of initial densities and empirical estimates of reproductive asynchrony. We also considered how protandry, a sexually selected life-history strategy that often accompanies asynchrony, modulates the population-level effects of reproductive asynchrony. We found that asynchrony decreases the number of males a female overlaps with, decreases the average probability of mating per male/female pair that does overlap, and leaves some females completely isolated in time. This loss of reproductive potential, which is exacerbated by protandry, reduces population growth rate at low density and can lead to extinction via an Allee effect. Thus reproductive asynchrony and protandry, both of which can be evolutionarily advantageous at higher population densities, may prove detrimental when population density declines.

Keywords: phenology, reproductive timing, protandry, extinction risk, bet hedging, life-history traits.

Maintaining mate-finding efficiency at low population density is of paramount importance to both individual fitness and population persistence. Reduced mate-finding efficiency at low density can cause an Allee effect, where population growth rate is an increasing function of population density (Allee et al. 1949; McCarthy 1997; Wells et al. 1998). Such inverse density dependence may select for increased mate-finding efficiency by favoring individuals that aggregate spatially or employ more efficient mate-location strategies. However, if traits affecting mate-finding efficiency cannot evolve quickly enough in response to this selection pressure, an Allee effect can translate into a lower critical density (termed the "Allee threshold") below which population growth rate becomes negative, dooming the population to extinction. If λ is the finite annual rate of increase under conditions of perfect mate finding, the Allee effect can be demonstrated phenomenologically in the context of a geometric growth equation

$$N_{t+1} = \lambda N_t[1 - q(N)], \tag{1}$$

where N is female population density and q is the proportion of females that go mateless (assumed constant across time for a given density). The population will decline to extinction when

$$q(N) > \frac{(\lambda - 1)}{\lambda}. \tag{2}$$

Mate finding is generally considered from a spatial perspective, where concerns about the relative locations of male and female individuals or gametes are the focus (McCarthy 1997; Groom 1998; Wells et al. 1998). In this view, high population density results in higher encounter rates among potential mates. In contrast, temporal variation in effective population size has been largely neglected in considerations of mate-finding efficiency. Nevertheless, the framework provided by equations (1) and (2) makes clear that isolation in time could lead to an Allee effect in the same way as isolation in space.

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Reproductive asynchrony, which occurs when individuals are reproductively active at different times within a larger population-level reproductive period, could cause Allee dynamics by reducing the temporal overlap of potential mates. To see this, assume that the probability that a given female and male mate is proportional to their temporal overlap (where d is their maximum possible temporal overlap), and that for each female, each encounter with a male is an independent event and does not influence her probability of mating with any other male. Assume further that females need mate only once to reproduce fully. The probability that a female does not mate, given encounters with n males, is then

$$P(\text{not mating}|n \text{ males}) = \prod_{i=1}^{n}\left[1 - \left(\frac{\text{overlap}_i}{d}\right)\right], \quad (3)$$

which can be large when n is small (low density) and approaches 0 when n is large (high density). Though several authors have suggested this possibility (Waldbauer 1978; Augspurger 1981; Bullock and Bawa 1981), the interactive effects of asynchrony and population density on population dynamics and extinction risk have not yet been studied in detail.

Reproductive phenology, in general, is frequently under strong natural and/or sexual selection and could influence population dynamics and extinction risk because it is often a key determinant of individual reproductive success (del Castillo and Nunez-Farfan 1999; Satake et al. 2001). To date, both theoretical and empirical studies of within-season reproductive phenology have focused on the selective pressures that favor synchronous or asynchronous reproductive strategies in populations where density is not an issue. Some of these have focused on natural selection acting on asynchrony among individuals (Augspurger 1981; Iwasa and Levin 1995; Ollerton and Diaz 1999; Post et al. 2001; Satake et al. 2001), whereas others have focused on sexual selection for asynchrony between the sexes, usually in the form of protandry (Wiklund and Fagerström 1977).

Studies on asynchrony among individuals have found that in a temporally unpredictable, coarse-grained environment, reproductive asynchrony ensures that some individuals of an asynchronous genotype attempt to reproduce at a favorable time during the breeding season each year. Much of the population-level variance in reproductive timing in this type of bet-hedging strategy is the product of alternative phenotypes of a given genotype and not of a polymorphism for maturation time (Rossiter 1991; Simmons and Johnston 1997; Tammaru et al. 1999). An evolutionarily stable distribution of maturation times can result from a single genotype expressing a variety of phenotypes that mature on different dates (Satake et al. 2001). Such "coin-flipping" plasticity in reproductive timing maximizes a genotype's geometric mean fitness over multiple generations (Cooper and Kaplan 1982; Seger and Brockmann 1987; Philippi and Seger 1989; Satake et al. 2001). Furthermore, theory predicts (Iwasa and Levin 1995; Satake et al. 2001) and empirical results confirm (Post et al. 2001) that asynchrony increases with the magnitude of large-scale, temporally unpredictable environmental disturbance.

Protandry, where modal reproductive maturity of males precedes that of females, can be advantageous to males when females mate only once and males must compete for receptive females (e.g., Wiklund and Fagerström 1977; Iwasa et al. 1983; Stephenson and Bertin 1983). Under these conditions, protandry increases a male's chance of successfully mating and can therefore be strongly favored via sexual selection. However, by separating male and female modal maturation times, protandry could aggravate temporal separation of potential mates at low density and thus may intensify any population-level effects of reproductive asynchrony among individuals.

For asynchrony to be advantageous, a population's effective density must remain high enough throughout the breeding season that opposite-sex individuals overlap with one another in time. Reproductive asynchrony thus creates a tension between spreading risk in an unpredictable environment and maintaining enough temporal overlap of potential mates throughout the breeding season to ensure reproductive success (Waldbauer 1978).

Here we explore the population-dynamic consequences of reproductive asynchrony as a density-dependent life-history trait. We assume that the degree of asynchrony in a population remains constant as population density declines because we found no data in the literature quantifying how heritable variance in reproductive timing might be nor how reproductive asynchrony might evolve in response to rapid changes in population density. Exploring the evolutionary dynamics of reproductive asynchrony as population density changes is a good next step, but it is beyond the scope of this article. Instead, we focus on demographics to explore the potential of asynchrony to affect small populations. We use a general model of reproductive timing to quantify the temporal overlap of opposite-sex individuals in a population as a function of asynchrony. Empirical data on reproductive timing from a range of asynchronous species, some of which are also protandrous, allow us to restrict our analyses to biologically relevant levels of asynchrony. We find that reproductive asynchrony among individuals can decrease a population's growth rate at low densities and induce an Allee effect; even small amounts of protandry can exacerbate these effects. In real systems, the population-level consequences of asynchrony will depend on how responsive traits affecting reproductive phenology are to selection at low population density, with both an increased risk of extinction or increased reproductive synchrony as possible outcomes. In either case, asynchrony among individuals and asynchrony between the sexes, both of which can be strongly favored in high-density conditions, appear to be critical but little-studied factors at low density.

Methods

Compilation of Empirical Data on Reproductive Timing

We conducted a literature search to identify representative species for which the timing of reproductive events has been studied in detail (table A1 in the appendix in the online edition of the *American Naturalist*). We recorded the duration of the reproductive period at both the individual and population levels. When data were available, we recorded the individual reproductive period for each of the sexes separately. For insects, information on the timing of individual reproductive activity was generally not available. Instead, we assumed that the individual reproductive period was equal to adult life span or residence time. Insofar as some individuals may not be capable of reproducing throughout their entire adult life or residence in a population, these data overestimate the length of the individual reproductive period, making our estimates of asynchrony somewhat conservative. We quantified the degree of asynchrony in these species as the ratio of the individual-level reproductive period to the population-level reproductive period. When applicable, we also recorded the extent of protandry in the population.

The types of empirical data underlying published reports on species' phenologies vary widely among authors. For example, some studies report the mean or median duration of reproductive activity while others report ranges. Because such differences may affect the accuracy of our estimates of the degrees of asynchrony and protandry in these species, we explicitly report in table A1 the types of data used to characterize species' phenologies. Despite these methodological uncertainties, it is clear that wide discrepancies exist between individual-level and population-level phenologies in many natural populations. Overall, our goal was to use this phenological data set to constrain our mathematical analyses to a range of realistic levels of asynchrony and protandry, not as a basis for precise, quantitative studies of particular species.

Development of a Reproductive Timing Model

We focused directly on the effects of an asynchronous life history and thus intentionally omitted other factors that may affect small populations, such as inbreeding depression and skewed sex ratios. We first addressed asynchrony among individuals and later added protandry. For simplicity, we separated the problems of quantifying the effects of asynchrony on a population's reproductive potential and quantifying its effects on population dynamics. First, we developed a static model that builds asynchronous populations for a given set of parameters and then records several statistics that quantify the loss of reproductive potential due to asynchrony. We then developed a dynamic model that incorporates geometric population growth and recorded the probability of extinction due to reproductive asynchrony across replicate populations for each parameter set.

Both the static and dynamic models have a stochastic element in that we dealt with random draws of individual phenologies from a larger population of possibilities. We used the stretched beta distribution (Hastings and Peacock 1975; Morris and Doak 2002) to represent the distribution of times at which individuals within a population become reproductively mature. The probability density function of the stretched beta distribution is

$$\beta(x|\nu, \omega, M) = \frac{1}{MB(\nu, \omega)}\left(\frac{x}{M}\right)^{\nu-1}\left(\frac{M-x}{M}\right)^{\omega-1}, \qquad (4)$$

where ν and ω are shape parameters controlling the distribution; M (days) is the total duration of the population's reproductive maturation period, from day 0 when the first individual becomes reproductively active to day M when the last individual in the population initiates its reproductive activity; and $B(\nu, \omega)$ is the beta function with parameters ν and ω:

$$B(\nu, \omega) = \int_0^1 u^{\nu-1}(1-u)^{\omega-1}du. \qquad (5)$$

An advantage of the stretched beta distribution is that the maturation times can be completely constrained to finite intervals while retaining extensive flexibility in shape (fig. 1). With this modeling approach, we assume that species-level traits determine both the length of the population-level reproductive maturation period (M) and how concentrated maturation events are within that period.

In both models, we first considered nonprotandrous populations where male and female beta distributions were identical and overlapped completely (asynchrony among individuals). We drew reproductive maturation times of individuals at random for populations with N_f females and N_m males (where N is population density and $N_\text{f} = N_\text{m}$, thus fixing the sex ratio at 1 : 1) and male and female beta

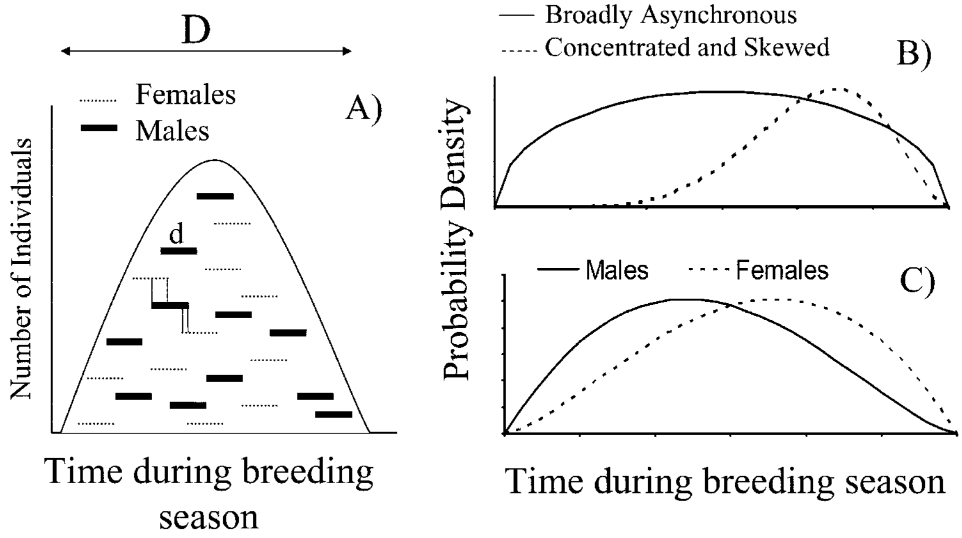

Figure 1: Schematic diagram of reproductive asynchrony. *A*, Relationship between individual and population-level reproductive periods (d and D, respectively). Horizontal bars represent male and female individual reproductive activity periods, whereas vertical bars demonstrate how one would quantify overlap between individual males and females. *B*, Stretched beta distribution is flexible enough to treat situations in which reproductive activity is broadly asynchronous ($\nu = \omega = 1.5$) or concentrated and highly skewed ($\nu = 1.5, \omega = 2.5$). *C*, Stretched beta distribution can be used to study protandry by generating different distributions for male and female reproductive activity.

distribution parameters $\nu = \omega = 1$ and then $\nu = \omega = 4$ (fig. 1). When $\nu = \omega = 1$, the beta distribution is formally equivalent to the uniform distribution (Hastings and Peacock 1975), and individuals are evenly distributed throughout the population-level maturation period M. For $\nu = \omega > 1$, a mid-season peak in maturation exists, and this peak becomes more strongly pronounced with further increases in the governing parameters. Once the reproductive maturity time for an individual was drawn, d, the duration of the individual reproductive period, was added to it to obtain each individual's reproductive activity period. This process was repeated until the reproductive activity periods of all individuals in the population had been determined. We defined the population-level breeding period, D (days), as the length of time during which a nonzero probability of individual reproductive activity exists, which is $D = M + d$. Though the total densities of males and females were kept equal each season ($N_f = N_m$), the sex ratio at particular times within a breeding season could fluctuate because individual activity periods were defined by randomly chosen, beta-distributed initiation times.

For each set of beta parameters, we examined reproductive asynchrony by varying the population-level maturation period M across 19 levels between 5 and 50 days. We fixed d at 5 days for both males and females, assuming that finite resource stores or accumulated damage (e.g., wing wear in butterflies or flower injury in plants) would constrain individuals' reproductive activity. The assumption of equal male and female d is justified based on the empirical data set (table A1), but in the discussion we describe the consequences of relaxing this assumption. We quantified the baseline potential for asynchrony in a population as the d/D ratio and thus could have obtained similar effects by fixing M and varying d. The d/D values we considered in our analyses were within the range of d/D values observed in the empirical data set (table A1). For each of the 19 levels of reproductive asynchrony, we built 500 replicate populations for each of 29 population densities ranging from 10 to 150 individuals per unit area.

In the static model, we tracked several measures of asynchrony and its effects. First, we quantified how reproductive asynchrony reduced temporal overlap of females with males at the population level. Summing individual overlaps across all female-male pairs, we calculated realized "reproductive overlap" as a proportion of maximum possible overlap (which is calculated as $N_f \times N_m \times d$). Reproductive overlap was then averaged over 500 replicate populations of each parameter combination. Second, we tracked the mean number of males that each female overlapped with in each population and then computed a grand mean across the 500 replicate populations. Third, for each population, we recorded the mean overlap for male/female pairs that had overlap >0 and then calculated a grand mean for this measure over the 500 replicates. Fourth, we recorded the coefficient of variation (CV) of the total temporal overlap of individual females with males within each population to characterize the degree of variability in overlap among females. These CVs were then averaged across replicate populations to obtain the mean CV of individual overlap. Fifth, to quantify the most extreme effects of reproductive asynchrony on a population's reproductive potential, we recorded the mean proportion of females that went mateless due to either complete temporal isolation from males or probabilistic failure to mate ($q(N)$ from eq. [1]). Once the fraction of mateless females was known for a particular replicate, we could calculate what reduction (if any) in population growth rate would be realized over a 1-yr interval.

Building off of the static model, the dynamic model considers populations that reproduce annually and have discrete, nonoverlapping generations, such as annual plants and many insects. For each parameter combination we conducted 500 replicate simulations of a stochastic variant of the simple discrete-time geometric population growth model given in equation (1). In our dynamic model, $q(N)$ is a stochastic term that varies among years based on randomly chosen phenologies of individual males and females. For each replicate each year, we probabilistically determined whether each female in the population would mate based on her temporal overlap with each of the males. Specifically, for each male-female pair, we defined the probability of mating as the pair's temporal overlap, in days, divided by d. A female needed to mate with only one male to enter the mated pool; multiple successful matings had no effect on fitness. (This constitutes a conservative assumption because fitness of female insects can increase with multiple matings [e.g., Oh 1979].) We set $\lambda = 1.03$ so that in the absence of stochastic effects attributable to reproductive asynchrony, the population would grow at a reasonably fast rate. Notice that no density dependence or predetermined Allee threshold is built into this population growth model; equation (1) has no functional dependence on density, and the parameters d, D, ν, and ω are assumed independent of density. The shape of the stochastic function $q(N)$ is a consequence of an interaction between asynchrony and population density. In these simulations, we focused on the dynamic consequences of reproductive asynchrony, recording the proportion of the 500 replicate populations that went extinct within 100 yr (beyond which time extinction was unlikely to occur because of our assumption of geometric growth).

Finally, we considered the combined effects of asynchrony among individuals and protandry on a population's reproductive potential and dynamics. To simulate protandry, we manipulated the shape parameters of the male and female beta distributions such that modal reproductive maturity occurred earlier for males than for females. The mode of the beta distribution, with M scaled to 1 day, is (Hastings and Peacock 1975)

$$\text{mode} = \frac{(\nu - 1)}{(\nu + \omega + 2)} \text{ for } \nu, \omega > 1. \tag{6}$$

Rescaling yields the actual extent of protandry in the population for each parameter combination. Because rescaling affects the total number of days of protandry for a given set of shape parameters, we used a numerical direct search routine to identify parameter combinations that yielded exactly two days of protandry for all values of M (table A2 in the online edition of the *American Naturalist*). Otherwise, we used the same parameters and the same analyses in both the static and dynamic models as above. This approach allowed us to compare asynchronous populations with and without protandry.

Results

Empirical Data

We found data on the reproductive phenologies of 21 species, including 16 butterflies, a bee, a stonefly, and three flowering plants (table A1). A wide range of reproductive asynchrony (defined as the d/D ratio) was apparent with the lowest degree being 0.52–0.82 for the self-incompatible perennial *Discaria toumatou* and the maximum being 0.02–0.05 for the monoecious (though rarely selfing) annual *Arum maculatum*. Insects spanned a slightly narrower range of d/D from the largely synchronous 0.45 (females) and 0.60 (males) stonefly *Megarcys signata* to the highly asynchronous 0.04–0.24 (females) and 0.05–0.13 (males) butterfly *Mellicta athalia*. On the basis of these data, we restricted our analyses to d/D of 0.33–0.09, which falls inside the natural range. Male and female phenologies differed for 11 of the 21 species, but quantitative data were available for only five species. Among this subset of species, the degree of protandry ranged from −1 (technically protogyny) to 21 days. To be conservative, we used only a 2-day separation between the modes of male and female reproductive activity in our modeling.

Measures of Reproductive Asynchrony

Reproductive asynchrony can decrease the number of mating opportunities in a population by reducing the mean temporal overlap of potential mates. For a given combination of the beta parameters ν and ω, holding the individual d constant while increasing the population D decreases mean reproductive overlap (fig. 2). However, when expressed as a proportion of the maximum possible overlap, the reduction in reproductive overlap remains constant across the population densities we considered and appears to be an intrinsic feature of that population's level of asynchrony (determined by d/D and the parameters of

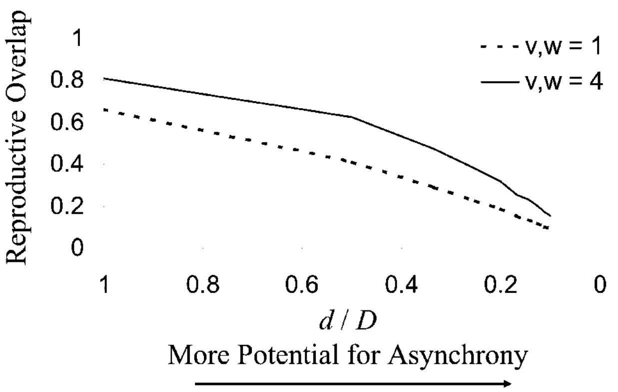

Figure 2: Reproductive overlap as a function of asynchrony for even ($\nu = \omega = 1$) and peaked ($\nu = \omega = 4$) maturation distributions. Reproductive asynchrony increases with decreasing d/D ratio.

the beta distribution; fig. 3*A*). This independence of density arises because both the maximum possible overlap and the realized overlap scale as functions of $N_f \times N_m$.

Although proportional overlap itself is density independent, the reduction in reproductive potential that it causes behaves in a density-dependent manner. Reproductive asynchrony acts in three ways to reduce reproductive potential through effects on temporal overlap. First, asynchrony reduces the mean number of males with which each female in the population overlaps in time (fig. 3*B*). Second, a decrease in total reproductive overlap in the population also decreases the average overlap (relative to the maximum possible pairwise overlap [i.e., d]) of those male/female pairs that do overlap in time. Because we have defined the probability of mating per male/female pair in the population as the realized proportion of their maximum possible overlap, asynchrony increases the number of females in the population that are mateless due to probabilistic failure to mate. Finally, at low population densities (generally <20 individuals/unit area but dependent on d/D), some females are mateless by virtue of complete temporal isolation. These three effects conspire to increase $q(N)$, the mean proportion of females that fail to reproduce as density declines in an asynchronous population (fig. 3*C*).

The coefficient of variation of female overlap with males increases with the level of asynchrony in the population and with decreasing population density (fig. 3*D*). This variability in overlap among females can be considered a form of demographic stochasticity. At population densities where the CV begins to climb rapidly in the static model (fig. 3*D*), populations have already gone extinct in the dynamic model, suggesting that interindividual variability in overlap modulates, but does not drive, the observed extinction dynamics.

The consequences of altering ν and ω to manipulate the shape of the reproductive maturation distributions for a given d/D ratio were weak compared with manipulating the d/D ratio for a given distribution shape. When d/D was held constant, spreading individuals more evenly across the breeding season ($\nu = \omega = 1$) slightly decreased mean reproductive overlap, exacerbating the negative effects of asynchrony relative to the case where individuals were more concentrated in time ($\nu = \omega = 4$; fig. 3*A*). Similarly, for a given d/D ratio, spreading individuals more evenly across the breeding season slightly increased the CV of overlap among females (fig. 3*D*). Thus, the shape of the reproductive maturation distribution acts only to modulate the effects of asynchrony determined by the d/D ratio.

Effects of Asynchrony on Population Growth Rate and Extinction Risk

The proportion of mateless females, $q(N)$, in the population directly affects realized population growth rate, which in turn determines the probability of extinction in the dynamic model. Because increases in D for a fixed d increase mean $q(N)$, increasing D strongly reduces mean realized growth rate over 1-yr intervals (fig. 4*A*, 4*B*) and increases the fraction of replicate populations in decline during a given time step (fig. 4*C*, 4*D*). The effects of asynchrony on population dynamics scale nonlinearly with density in that a given increase in D has larger consequences for small populations than for large (to see this, note that the contour lines in fig. 4 are not parallel). The predominance of d/D over (ν, ω) is also apparent in figure 4. For a given d/D, shifting from a broadly asynchronous reproductive distribution of reproductive activity ($\nu = \omega = 1$) to a distribution that is quite concentrated in time ($\nu = \omega = 4$) makes only small changes to the slopes of the contour lines describing realized growth rate (cf. fig. 4*A*, 4*C* with fig. 4*B*, 4*D*).

For the most extreme levels of asynchrony we considered ($d/D = 0.09$), populations regularly went extinct at total densities (males + females) of 70–80 individuals/unit area (fig. 5). Even for minimal levels of asynchrony ($d/D = 0.33$), populations still regularly went extinct at total densities of 10–20 individuals/unit area. Thus, even acting alone, loss of reproductive potential due to asynchrony among individuals can drive an otherwise growing population extinct. The shape of the probability of extinction profiles is consistent with the expectation that reproductive asynchrony causes an Allee effect (fig. 5). This result is also in agreement with other studies of reduced mating efficiency at low population density, but because

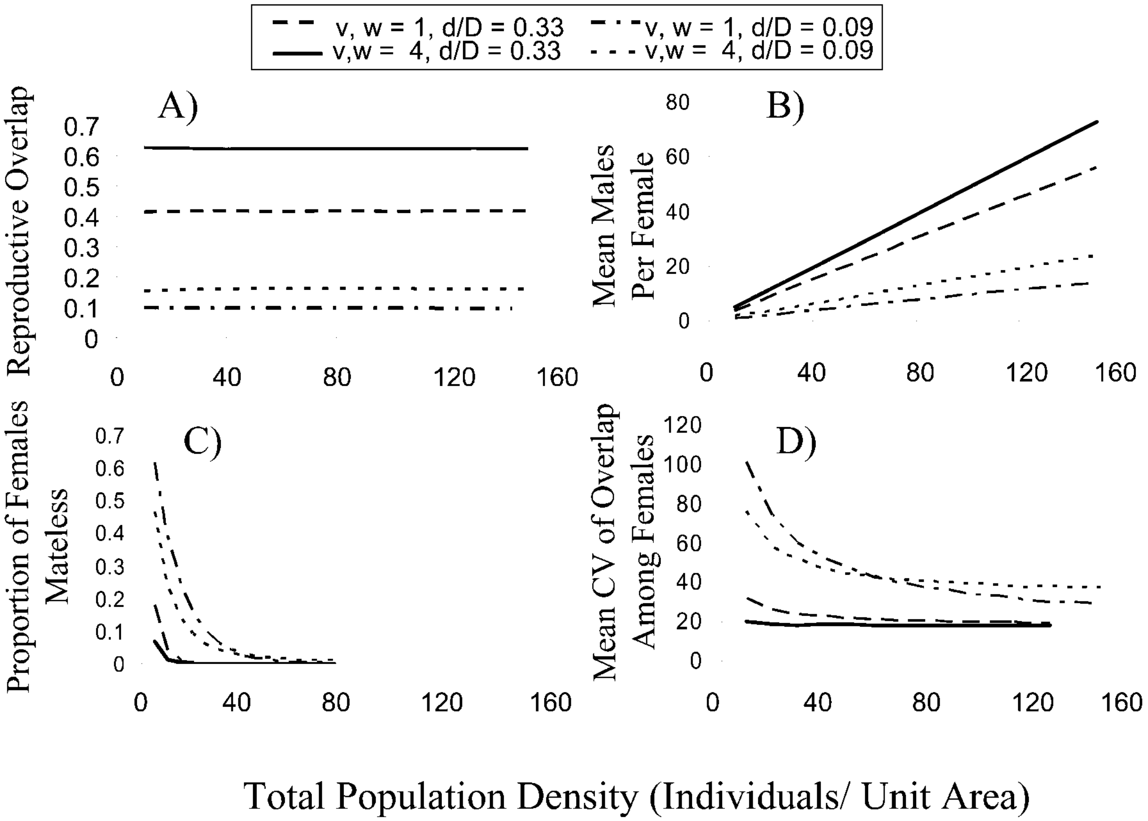

Figure 3: Consequences of asynchrony for reproductive success. *A*, Proportional overlap differs for each level of asynchrony (beta parameters and *d*/*D* ratio) but, for a given combination of parameters, remains constant over the range of population densities considered. *B*, Mean number of male and female overlaps within populations characterized by different levels of asynchrony. An increase in reproductive asynchrony decreases the slope of the relationship between mean number of males per female and population density. *C*, Average proportion of females in the population that are mateless due to reproductive asynchrony. Failure to mate increases sharply with decreasing population density and with increasing degrees of asynchrony in the population. *D*, Among-female variability in reproductive overlap with males. Variability increases with decreasing population density and with increasing levels of asynchrony. Changes in the beta parameters and thus the variance of maturation distributions for a given *d*/*D* had only minor effects on variability.

our model includes stochasticity in $q(N)$, there was no specific Allee threshold per se. Instead, in all cases, a population's probability of extinction transitioned from 0 to 1 over a small range of density (fig. 5). The *d*/*D* ratio had the strongest effect on a population's probability of extinction, whereas manipulating the shape parameters of the beta distributions for a given *d*/*D* had small effects on the probability of extinction (fig. 5).

Effects of Asynchrony on Protandrous Populations

Protandry, as expected, exacerbates the negative effects of reproductive asynchrony among individuals by further reducing mean reproductive overlap between potential mates. As an example, consider a population with $d/D = 0.2$, male $\nu = 3.86$, $\omega = 3.14$, and female $\nu = 3.14$, $\omega = 3.86$. These parameters result in male and female maturation distributions that are symmetrical with respect to one another and feature 2 days of protandry (based on the difference in modes of the distributions). Even this minimal level of protandry negatively affects reproductive overlap relative to nonprotandrous populations with similar shape parameters (fig. 6*A*). Protandry had comparable effects on populations across a range of *d*/*D* values, relative to similar nonprotandrous populations (results not shown). For a given population density, the extra reduction in reproductive potential due to protandry increases a population's risk of extinction compared with a population that is asynchronous but not protandrous (fig. 6*B*). Thus, protandry can act synergistically with asyn-

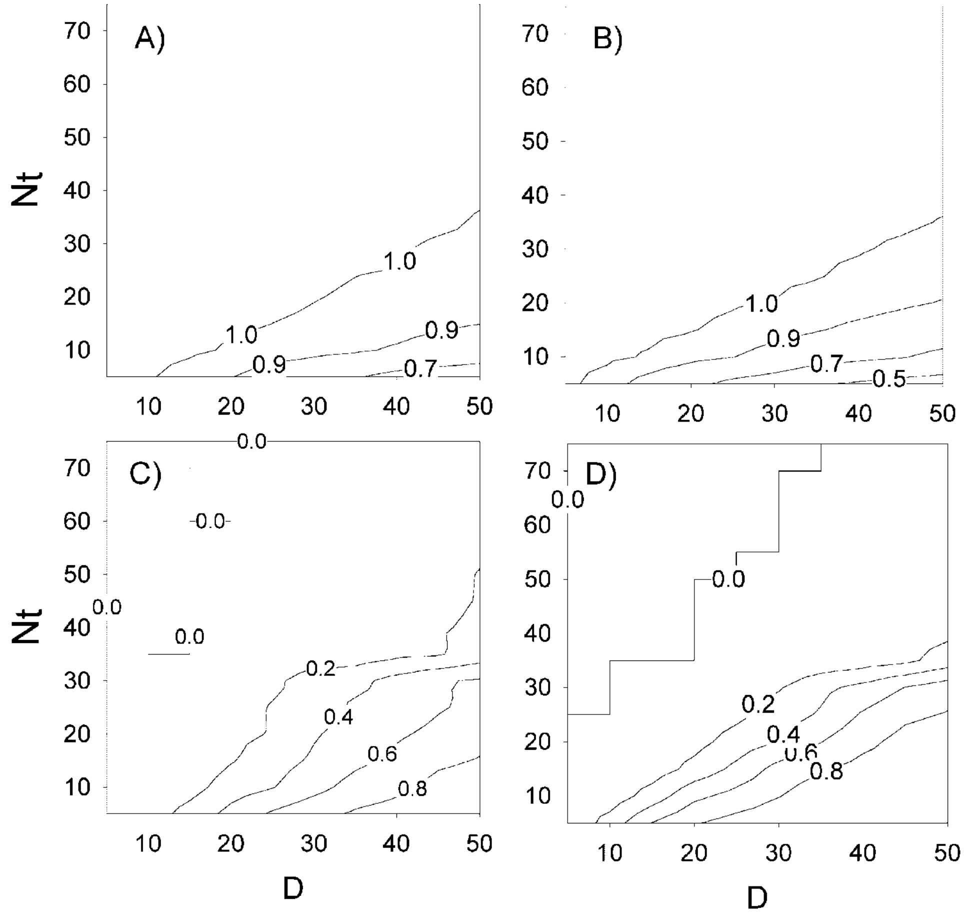

Figure 4: Joint effects of population density and the duration of population-level reproductive period on realized population growth rate. *A* and *B* provide contours of realized population growth rate (arithmetic mean across 500 replicates). Values <1.0 correspond to populations that would on average decline due to reproductive asynchrony. *C* and *D* provide contours of the proportion of 500 replicate populations with realized population growth rate <1.0. *A* and *C* are for populations with uniform distributions of reproductive activity ($\nu = \omega = 1$) whereas *B* and *D* represent populations with a midseason peak in reproductive activity ($\nu = \omega = 4$).

chrony among individuals to increase the risk of extinction at low population density.

Discussion

Anthropogenically driven declines of many species have forced ecologists and evolutionary biologists to consider density dependence in the population-level effects of life-history traits. Such analyses can both identify life-history traits that may influence population persistence (Pimm et al. 1988; Saether 1997; Fagan et al. 2001; Johnson 2002; Green 2003) and highlight selection pressures that can affect life-history evolution. Though reproductive asynchrony—either among individuals or between the sexes—can be advantageous at high density, we have demonstrated here that it can have hidden consequences at low population density. We found that biologically realistic levels of reproductive asynchrony (table A1) reduce the reproductive potential of the population by decreasing the temporal overlap of potential mates. Reduced mating efficiency at low population density, regardless of the specific mechanism that causes it, leads to an Allee effect (McCarthy 1997).

The Allee effects observed in this study emerge from the interaction of population density with reduced mating efficiency caused by variable reproductive timing among individuals; they do not derive from a predetermined Allee threshold in our population growth model. Instead, reproductive asynchrony itself acts as a mechanism generating the Allee effect. Specifically, a female's total probability of mating within a breeding season depends on the density of males during her reproductive activity period.

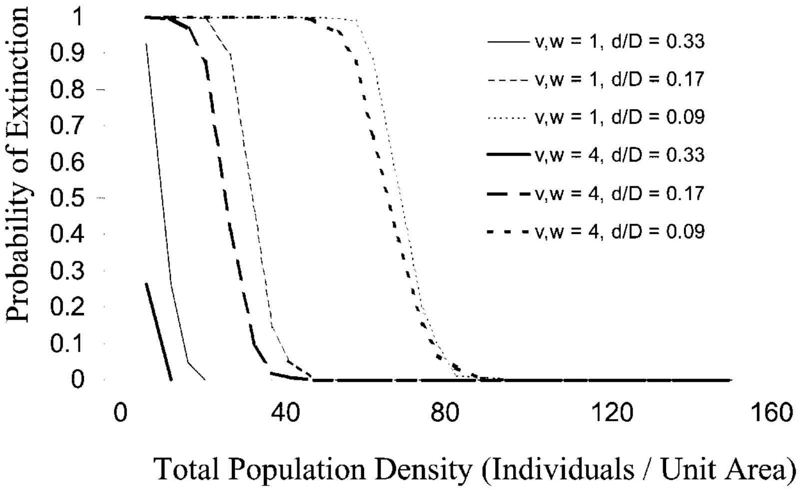

Figure 5: Extinction risk profiles for various levels of asynchrony. A population's *d*/*D* ratio was the main determinant of extinction risk for that population. Changes in the variance of the maturation distributions for a given *d*/*D* ratio had minor effects.

Male density at any point during the breeding season, in turn, is affected by both the total male population density and the temporal distribution of male reproductive activity across the breeding season. Reproductive asynchrony therefore satisfies the criterion of inverse density dependence at low population density necessary for the operation of an Allee effect (Courchamp et al. 1999). Accordingly, both realized population growth rate (fig. 4) and extinction risk are affected (fig. 5).

Variability among females in total reproductive overlap due to sampling effects at small population densities can be considered a form of demographic stochasticity. It causes the realized population growth rate contours to be "messy" (fig. 4) and the (0, 1) step function for extinction probability in deterministic Allee effect models to be "blurred" into a sigmoidal curve that decreases as a function of population density (fig. 5; see also Boukal and Berec 2002). Several authors have noted this "stochastic blurring" effect in models that explicitly include both Allee effects and demographic stochasticity (Dennis 1989, 2002; Berec et al. 2001). Stochastic Allee effects are characterized by a probability of extinction versus initial population density curve that exhibits an inflection point and a sharp transition in the probability of extinction near that inflection point (Dennis 1989, 2002; Boukal and Berec 2002). These patterns differ markedly from the dynamic characteristics of demographic stochasticity alone, in which the probability of extinction increases smoothly and gradually with decreasing population size (Dennis 2002). Populations suffering from an Allee effect induced by reproductive asynchrony are therefore more likely to exhibit sudden crashes than those suffering from demographic stochasticity per se.

Protandry, which separates the modal maturation times of males and females within a population, clearly exacerbates the effects of reproductive asynchrony among individuals, placing populations at greater risk of extinction for a given density (fig. 6). Even the minimal degree of protandry we considered (2 days) had significant effects on a population's probability of extinction. Empirical data suggest that protandry can be far more extreme (table A1). For example, the meadow brown butterfly *Maniola jurtina* had approximately 21 days of protandry and a *d*/*D* ratio between 0.11 and 0.2. It must be recognized, however, that *M. jurtina* is a common, and occasionally abundant, species, and it is not clear that such extreme protandry would persist in small populations. Indeed, the density dependence of protandry appears to be quite open as an area of inquiry.

The timing of the initiation of male reproductive activity is frequently under strong sexual selection in populations of butterflies (Wiklund and Fagerström 1977; Wiklund and Solbreck 1982; Iwasa et al. 1983), dioecious plants (Purrington 1993; Purrington and Schmitt 1998), and other species (e.g., del Castillo and Nunez-Farfan 1999; Holzapfel and Bradshaw 2002). Consequently, the same kinds of species that feature major discrepancies between individual- and population-level reproductive periods (i.e., small *d*/*D* ratios) frequently exhibit significant protandry (table A1). Several recent articles have noted the potential influence of certain sexually selected traits on extinction risk, but none, to our knowledge, has dealt

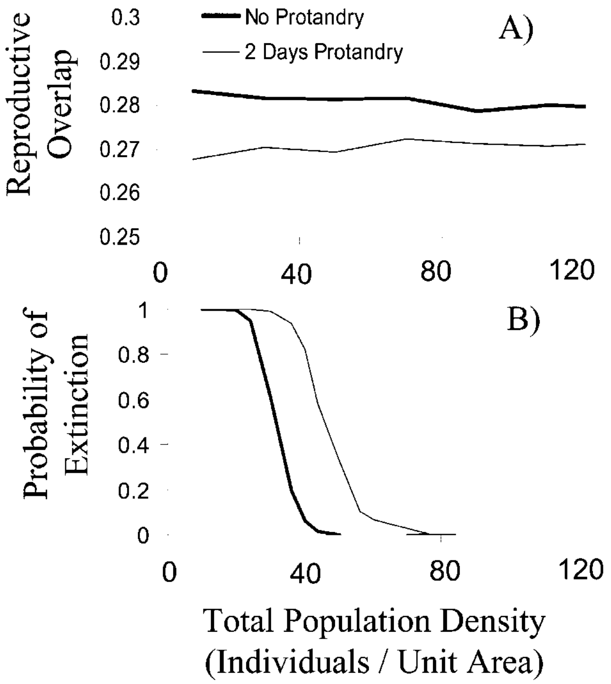

Figure 6: Effects of protandry on reproductive overlap and extinction risk in populations with reproductive asynchrony. *A*, Reproductive overlap for a population with 2 days of protandry (male $\nu = 3.86$, $\omega = 3.14$; female $\nu = 3.14$, $\omega = 3.86$) and a population with no protandry (male and female $\nu = \omega = 3.14$). For both populations, $d/D = 0.2$. *B*, Extinction risk profiles for a population with 2 days of protandry and a population with no protandry (parameters as in *A*).

with the added risks associated with sexual selection acting on phenology (Doherty et al. 2003; Kokko and Brooks 2003; Møller 2003). The potential to explore issues such as phenology that may differ between males and females is one advantage of working with two-sex models when examining extinction risk (see also Engen et al. 2003).

Clearly, a variety of changes to the model, such as making λ larger, making the sex ratio consistently male biased, or lengthening male *d* relative to female *d*, will lessen the severity of the loss of reproductive potential caused by asynchrony. For example, consider that in many species, a few individuals will have long individual reproductive periods, while most individuals hover close to the population mean. Adding this kind of interindividual variability in *d* would likely decrease the negative effects of asynchrony but would require additional model complexity relating to individual senescence or limits on the number of matings per male per unit time or per lifetime. Still, our results show that even when all individuals in the population are long-lived (high *d*/*D* ratio), asynchrony reduces a population's growth rate and elevates its extinction risk relative to a synchronously breeding population. In contrast to the above suite of factors that could lessen the effects of asynchrony, any spatial processes that reduce effective population density, such as limited search area or imperfect mate-locating ability, will exacerbate the effects of asynchrony.

Additional development of this modeling framework is warranted to explore its sensitivity to assumptions we made concerning density independence of the key parameters *d* and *D* and the emphasis on annual life cycles. For example, if individual reproductive timing is highly heritable, then *D* could narrow with decreasing density because those females that were closely synchronized with the bulk of the male population would be more likely to reproduce. Although numerous experimental studies, especially in plants, have assessed heritability of the date of first reproduction (Matziris 1994; Kelly and Levin 1997; Nikkanen 2001; Tikkanen and Lyytikainen-Saarenmaa 2002), the degree to which variance in reproductive timing is heritable appears little explored. Likewise, the degree to which individual *d* can evolve in response to selection for more synchronized reproduction at low densities appears worthy of study. Another obvious extension would be to explore the dynamic consequences of reproductive asynchrony in perennial populations. Quantifying the effects of reproductive asynchrony in perennial species would require modifying the population growth model we employed (e.g., shifting the focus to geometric average growth rates per generation). However, the phenomenon seems likely to remain important because, even in perennial species, reproductive asynchrony could reduce an individual's lifetime reproductive success and alter population-level recruitment patterns.

Other authors have noted potential effects of asynchrony on populations of insects (Waldbauer 1978), plants (Primack 1980; Augspurger 1981; Ollerton and Diaz 1999), the maintenance of both plant-pollinator mutualisms (Anstett et al. 1995) and host-parasitoid interactions (Godfray et al. 1994), but none has studied quantitatively the density-dependent effects of asynchrony per se on population growth and extinction risk. Our results demonstrate that reproductive asynchrony may strongly affect low-density populations, particularly when the ratio of the individual-level reproductive period to the population-level reproductive period is less than one-third. Several species in our analysis exhibit population parameters that, in our model, cause considerable decreases in population growth rate and make a population quite vulnerable to extinction at low density (table A1). Acting alone or synergistically with life-history traits such as protandry, reproductive asynchrony among individuals can reduce population growth rate and increase extinction risk.

The severity of these effects may hinge on how quickly traits affecting individual reproductive timing can respond to selection for reproductive synchrony at low density. A quick response at low density could serve as a buffer against the negative effects of asynchrony, permitting variable populations to be more asynchronous at high density. In contrast, a slow response might allow the Allee effect to limit the degree of asynchrony that is advantageous in natural populations. It is ironic that reproductive asynchrony and protandry, both of which may be under strong positive selection at high density, may be quite disadvantageous to population persistence at low density. Taken to the extreme, reproductive asynchrony could provide another example of evolutionary suicide. Reproductive asynchrony should therefore be recognized as a mechanism of the Allee effect and be included among the suite of life-history characters analyzed when determining a species' extinction risk at low population density. More generally, the consequences of phenological variation among individuals have not received adequate attention in relation to population dynamics and extinction risk. It is clear from the literature that, as commonly used, "phenology" usually refers to population-level events such as the flight period in butterflies or blooming time in flowering plants. Our results highlight the importance of the distinction between the phenology of individuals and the phenology of populations and outline some of the consequences of this relationship for ecological systems.

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