

Linking the Allee Effect, Sexual Reproduction, and Temperature-Dependent Sex Determination Via Spatial Dynamics

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Received January 10, 2000; Accepted September 19, 2000

ABSTRACT: We develop a spatially explicit, two-sex, individual-based model (IBM) and a derived spatially homogeneous model (SHM) to describe the Allee effect due to scarcity of mating possibilities at low population sizes or densities. The SHM, based on coupled difference equations, represents the first spatially homogeneous approach to this phenomenon, which differentiates between sexes and relies only on measurable population parameters. The IBM reinforces the findings of the SHM by adopting more realistic mate search strategies of diffusive movement and active search. Both models are characterized by a hyperbolic-shaped extinction boundary in the male-female state space, which contrasts with a linear boundary in one-dimensional models of the Allee effect. We examine how the position of the extinction boundary depends on population demography (primary sex ratio, reproduction and mortality probabilities) and adopted mate search strategies. The investigation of different phases in the IBM dynamics emphasizes the differences between local and global densities and shows the importance of scale when assessing the Allee effect. To demonstrate the potential application of our models, we combine the SHM and available data to predict the impact of environmental temperature changes on two turtle species with temperature-dependent sex determination.

Keywords: conservation biology, extinction threshold, individual-based model, mate search strategy, turtle.

One of the central problems in conservation biology is to discover factors that maintain the viability of populations or cause their extinction. Knowledge of these factors may help to save species pushed to the verge of extinction, to

successfully introduce or reintroduce populations into new or original habitats, and to eliminate pests or unwanted invaders when their populations are still limited in numbers or distribution.

Reasons for population extinctions may be rather complex and difficult to reveal in a given case. Risk factors enhancing extinction probability include interactions with populations of other species (Murray 1990), demographic stochasticity (Legendre et al. 1999), environmental stochasticity and natural catastrophes (Lande 1993), mutation accumulation (Lynch et al. 1995), or the Allee effect, a term used to collectively describe any of the processes hypothesized to lead to a reduction in individual fitness at low population sizes or densities (Stephens and Sutherland 1999; Stephens et al. 1999).

Various mechanisms, such as reduced group defense against predators, reduced care for young, reduced foraging efficiency, or enhanced genetic inbreeding at low population sizes or densities, have been proposed as potential sources of the Allee effect (Lewis and Kareiva 1993; Sæther et al. 1996; Courchamp et al. 1999a; Stephens and Sutherland 1999). However, the most cited phenomenon that supposedly leads to the Allee effect is the difficulty in finding mates in small, sexually reproducing populations (Ehrlich and Roughgarden 1987; Levitan et al. 1992; Groom 1998; Kindvall et al. 1998; Wells et al. 1998; and others). Our review of the literature showed that all but one mathematical model of the Allee effect is one dimensional (Volterra 1938; Asmussen 1979; Jacobs 1984; Hopf and Hopf 1985; Dennis 1989; Lewis and Kareiva 1993; Fauvergue et al. 1995; Pfister and Bradbury 1996; Veit and Lewis 1996; Amarasekare 1998a, 1998b; Courchamp et al. 1999b), and the majority of them are extensions of the Verhulst's logistic model of a population growth. The common feature of these one-dimensional models is the existence of a bistable regime that leads the population either to extinction or to successful establishment, depending on the initial population density. The reaction-diffusion model by Hopper and Roush (1993) that differentiates

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Table 1: Parameters used in model descriptions

| Parameter | Meaning |
|---------------------|--|
| S | Lattice size (128×128) |
| p_r | Probability of reproduction per reproductive event |
| μ | Primary sex ratio |
| p_m^M (p_m^F) | Mortality probability of males (females) per time step |
| d_M (d_F) | Neighborhood size of males (females) with diffusive movement |
| s_M (s_F) | Perception neighborhood size of males (females) actively searching for mates |
| x_M (x_F) | Male (female) abundance or density at a given time step |
| x'_M (x'_F) | Male (female) abundance or density at the next time step with respect to x_M (x_F) |

between sexes resembles this behavior but established populations grow infinitely instead of approaching a saturation value. Spatially homogeneous models (SHM) of sexually reproducing populations found in the literature (Caswell and Weeks 1986; Lindström and Kokko 1998; Legendre et al. 1999) do not demonstrate the bistable pattern typical for the Allee effect.

Knowledge of extinction thresholds and their dependence on behavioral and/or demographic characteristics of organisms is essential in an effective design of conservation measures for threatened populations and species. A model rescue operation of a population supposedly subject to the Allee effect was successfully attempted, for example, for the Hawaiian goose *Branta sandvicensis* where nearly all scattered living individuals were collected and bred in captivity until the population had again reached a viable size (Kear and Berger 1980).

Using a spatially explicit approach, we developed a two-sex individual-based model (IBM) and a derived SHM to address the following questions: Does the population demonstrate the bistable pattern due to the scarcity of mating possibilities at low sizes or densities that is known from one-dimensional models? How do various demographic parameters and mate search strategies affect population dynamics? We show that the mate-finding Allee effect arises as an intrinsic characteristic of our models, and it is, unlike in the one-dimensional models, fully described by basic demographic parameters (primary sex ratio, reproduction, and mortality probabilities) and mate search strategies (diffusive movement and active search).

Primary sex ratio depends on incubation temperature of eggs in a number of reptiles (Paukstis and Janzen 1990; Janzen and Paukstis 1991; Girondot 1999). Environmental temperature changes could thus profoundly affect reptile populations subject to the combination of the Allee effect and this phenomenon, termed temperature-dependent sex determination (TSD). To demonstrate the potential application of our models, we use the SHM and available data to link incubation temperatures and population extinction/survival via primary sex ratio.

Model Formulations

Effects taking place at low population sizes or densities suggest that an individual is the most adequate population unit. Moreover, consideration of mate search strategies requires explicit modeling of both sex and space. In this section, we compose a spatially explicit IBM that keeps track of every single male and female in a spatial habitat during their entire lifetime (McCauley et al. 1993; Keeling 1999; McGlade 1999). As far as we are aware, no such IBM has been previously proposed. We also derive its spatially homogeneous counterpart that permits a more detailed analysis and comparison with known models. Parameters used in the models are summarized in table 1 and explained below.

Two-Sex Spatially Explicit IBM

A square lattice of 128×128 uniform sites approximates the homogeneous spatial habitat, with each site occupied by, at most, one male and one female. Periodic boundary conditions are used to mimic an unbounded environment so that the left and right edges and the top and bottom edges of the lattice are joined together. Time runs are conducted in discrete steps, in which all sites are simultaneously updated. Initially, individuals are (uniformly) randomly scattered over the lattice, with males and females distributed independently. Population processes consist of two parts that are repeatedly applied in a sequential way: demographic processes (reproduction and mortality) and mate search.

Reproduction. At every time step, each pair (male and female sharing a site) gives birth to one offspring with non-zero probability p_r . The conceived offspring becomes a male with probability $0 < \mu < 1$ (primary sex ratio) and a female with probability $1 - \mu$. It is placed into a randomly selected nearest neighbor of its parents' site if the selected site is free of an adult of the same sex. If two or more offspring of the same sex attempt to recruit to the same

site at the same time step, one of them is randomly chosen and allowed to do it, the rest discarded. Thus, reproduction is density dependent. Maturation time of each offspring is one time step.

Mortality. At every time step, each male and female die with probability p_m^M and p_m^F , respectively (background mortality). No other components of mortality are assumed to act in order to concentrate solely on the effects of mate search and to facilitate derivation of the SHM.

Reproduction and mortality operate concurrently (McCauley et al. 1993), that is, newborns cannot die at the same time step and adults that are marked as dead have the full opportunity to reproduce at that step. Once the demographic processes are accomplished, mate search is initiated. We consider two mate search strategies.

Diffusive Movement. An individual with this strategy moves independently of others to a randomly selected site in a square neighborhood of side $2d + 1$ ($d = 0, 1, 2, \dots$; $d = 0$ models sedentary individuals), centered on its location; if it is occupied by the same sex, the individual does not move. The neighborhood size may differ for males (d_M) and females (d_F) to allow for a range of movement rates.

Active Mate Search. We model actively searching individuals by a rule that is analogous to a bird flock search for suitable breeding sites (Fahse et al. 1998). Any such individual is assumed to have a square perception neighborhood of side $2s + 1$ ($s = 1, 2, \dots$) around its location due to, for example, detection of pheromones (insects, reptiles, rodents), advertisement calls (amphibians), or songs (birds) by the other sex. Let us consider a particular, actively searching male (the same rules apply to females). If a sole and partner-free female is present in his perception neighborhood, the male moves to her site. If he locates two or more unmated females at the same time step, one of them is randomly selected. If no such female is found, the male moves to a randomly selected site inside his perception neighborhood unless it is occupied by another male; otherwise, he does not move. The neighborhood size may differ for males (s_M) and females (s_F).

If a pair is formed while mate search is running, individuals of that pair no longer move at that time step. Moreover, male and female paired during the previous time step move independently, and irrespective of previous reproductive success or failure. This rule corresponds to a monogamous mating system with no fidelity. To apply each mate search rule, all individuals are randomly ordered and act sequentially. As a consequence, contests for mates do not occur. The reader is referred to McCauley et al.

(1993) for further technical issues of discrete-time and discrete-space IBM.

Spatially Homogeneous Model

The spatially homogeneous counterpart of IBM is derived under the assumption that individuals of each sex are randomly distributed on a sufficiently large lattice at each time step (among other things, this assumption implies random mating). Time evolution of mean population densities is then sufficiently approximated by the following system of coupled difference equations (see app. A for a derivation):

$$\begin{aligned} x'_M &= x_M(1 - p_m^M) + \mu p_r x_M x_F(1 - x_M), \\ x'_F &= x_F(1 - p_m^F) + (1 - \mu) p_r x_F x_M(1 - x_F), \end{aligned} \quad (1)$$

where x_M (x_F) and x'_M (x'_F) are male (female) densities at the actual and next time steps, respectively.

Analytical and Simulation Results

Spatially Homogeneous Model

In this section, we examine the SHM (1). Results are derived analytically unless stated otherwise. (More details on the underlying mathematical analysis are given in app. B and C.)

For all parameter combinations, populations with sufficiently small initial male and female densities become extinct. Moreover, there are either zero, one, or two nontrivial steady states. To map parameter regions corresponding to each of these three cases (fig. 1), we introduce compound parameters

$$A_M \equiv \frac{p_m^M}{\mu p_r} \quad \text{and} \quad A_F \equiv \frac{p_m^F}{(1 - \mu) p_r},$$

which are independent of the timescale.

If $\sqrt{A_M} + \sqrt{A_F} > 1$, there are no steady states with non-zero population densities. On the other hand, if $\sqrt{A_M} + \sqrt{A_F} < 1$, two distinct nontrivial equilibria appear. As we were unable to resolve the stability of the nontrivial equilibria analytically, we performed extensive simulations of the SHM (1) for $0 < A_M, A_F < 1$. We also varied demographic parameters for some fixed values of A_M and A_F . For each set of parameters, we chose a set of initial conditions that sufficiently covered the male-female state space. These simulations suggest that if no nontrivial equilibria exist, the origin E^0 is globally stable and the population always dies out regardless of initial male and female population densities. We shall call such systems extinction-

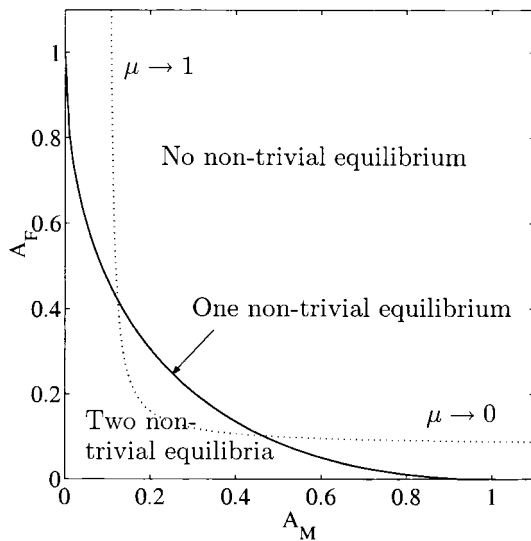


Figure 1: Compound-parameter space with regions of zero, one, and two nontrivial equilibria of the spatially homogeneous model (eq. [1]). The dotted line corresponds to the compound parameters A_M and A_F with $p_r = 0.1$, $p_m^M = 0.01$, $p_m^F = 0.008$, and primary sex ratio μ changing from 0 to 1. Points on the bold line satisfy $\sqrt{A_M} + \sqrt{A_F} = 1$.

doomed. If two nontrivial equilibria exist, we claim that the smaller equilibrium, denoted by $E^u = (x_M^u, x_F^u)$, is unstable (a saddle point), and that the larger steady state $E^s = (x_M^s, x_F^s)$ is locally stable. The simulations also showed that the system either approaches E^0 or E^s depending on initial conditions. We shall call such systems “extinction-survival systems” and the line separating the attracting regions of E^0 and E^s an extinction boundary. This gives an affirmative answer to the first question posed in the introduction: the bistable regime typical for the Allee effect appears.

Figure 2 shows the state space structure typical for parameters leading to two nontrivial equilibria. Note that a sharp decline in one sex or even in the total population size may not necessarily mean an ultimate population extinction. The hyperbolic-shaped extinction boundary contrasts with the straight line that arises if one-dimensional models are projected on the male-female state space (fig. 3). It is asymmetric with respect to the line $x_F = x_M$, except in the case of identical life cycles of both sexes (equal mortality rates in our model) with the balanced primary sex ratio $\mu = 0.5$.

Although the number and location of equilibria are fully described by the compound parameters A_M and A_F , we would have to take all demographic parameters into account if we needed to (numerically) locate the extinction boundary and to study transient dynamics of the SHM (1). Despite that, the areas of initial conditions leading to

extinction and survival can be partially characterized by the distance of E^u from the other two equilibria. The extinction (survival) area is positively related to the distance of E^u from E^0 (E^s) and enlarges (shrinks) with increasing A_M and/or A_F .

What are the effects of changing primary sex ratio μ on the system dynamics when mortality and reproduction parameters, p_m^M , p_m^F , and p_r , are kept fixed? Such a dependence may play a crucial role in species for which changing environmental conditions affect sex determination much more than other life-history characteristics (Charnov and Bull 1977). If reproduction is low,

$$\sqrt[3]{p_m^M} + \sqrt[3]{p_m^F} > \sqrt[3]{p_r}, \tag{2}$$

then the SHM (1) is extinction-doomed for all values of primary sex ratio μ ; different μ can only slow down or speed up the inevitable extinction process. For high reproduction rates,

$$\sqrt[3]{p_m^M} + \sqrt[3]{p_m^F} < \sqrt[3]{p_r}, \tag{3}$$

critical values $0 < \mu_1 < \mu_2 < 1$ exist such that extreme values of μ lying outside the interval (μ_1, μ_2) drive the system to extinction, whereas μ inside that range makes it an extinction-survival system.

If male and female mortalities are equal ($p_m^M = p_m^F$), conditions (2) and (3) reduce to $P > 1/8$ and $P < 1/8$, re-

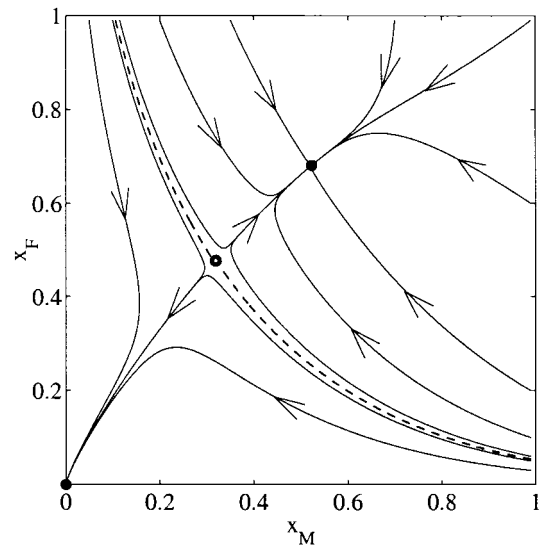


Figure 2: Sample invariant curves of the spatially homogeneous model (eq. [1]) in the male-female state space, showing equilibria (filled circle = stable, empty circle = unstable) and extinction boundary (dashed line). Arrows indicate the orientation of orbits belonging to each invariant curve. Parameter values: $\mu = 0.4$, $p_r = 0.1$, $p_m^M = 0.013$, $p_m^F = 0.01$.

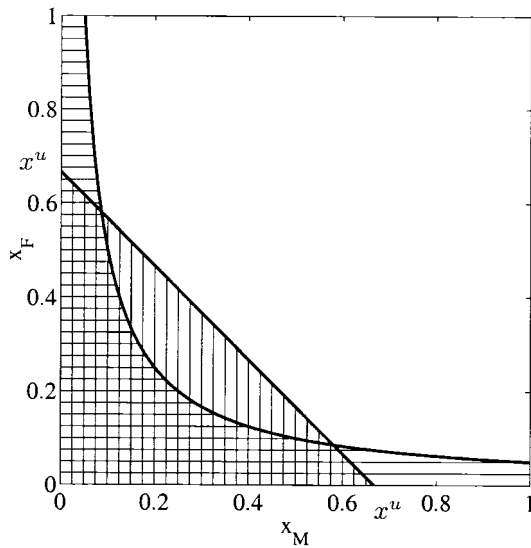


Figure 3: Schematic illustration of areas of initial male and female population densities (x_M , x_F) leading to extinction of the entire population in the spatially homogeneous model (eq. [1]) (horizontal lines) and a one-dimensional model artificially expanded to contain two sexes (vertical lines). Corresponding extinction boundaries are in bold; the boundary of the expanded one-dimensional model is the line $x_M + x_F = x^u$, connecting points $(0, x^u)$ and $(x^u, 0)$, where x^u is the unstable equilibrium of the one-dimensional model.

spectively, where $P \equiv p_m^M/p_r$ and the critical values μ_1 and μ_2 can be derived analytically. They are symmetrical with respect to the unbiased primary sex ratio $\mu = 0.5$:

$$\mu_{1,2} = \frac{1}{2} \left[1 \pm \sqrt{1 - 4P - 8P^2 - 8P\sqrt{P(1 + P)}} \right]. \quad (4)$$

The interval (μ_1, μ_2) leading to extinction-survival systems becomes larger with decreasing P , that is, with increasing reproduction p_r and/or decreasing mortality $p_m^M = p_m^F$. We observed analogous qualitative dependence also for different male and female mortalities.

We now use the SHM (1) and available data to predict the combined impact of TSD and the mate-finding Allee effect on the snapping turtle *Chelydra serpentina* and the European pond turtle *Emys orbicularis*. For both species, demographic characteristics have been quantitatively studied (Christiansen and Burken 1979; Obst 1986; Paukstis and Janzen 1990; Iverson 1991; Girondot and Pieau 1993). In *C. serpentina*, only females are produced at low as well as high egg incubation temperatures and only males are produced at intermediate temperatures, with two transitional ranges between these extremes; we found the original polynomial fit in Janzen and Paukstis (1991) unsatisfactory and replaced it by an exponential function (table

2; fig. 4A). In *E. orbicularis*, only males are produced at low egg incubation temperatures and only females at high temperatures, with a transitional range in which both sexes are produced; Girondot (1999) gives the exponential fit (table 2; fig. 4B).

We transform the field data (table 2) to fit our model using several compromising assumptions. The number of eggs per year is multiplied by the fraction of individuals achieving the reproductive age to get the number of new adults each year, and we divide this number into “single-individual reproductive events” by rescaling the time step (i.e., we assume that each female gives birth to one offspring per reproductive event with probability $p_r = 1.0$, and this offspring matures in one time step). Both assumptions in fact mean that we neglect possible effects of time lags in population dynamics; similar arguments have been adopted by Veit and Lewis (1996). The annual adult mortality is recomputed to the per time step adult mortality; as there is no distinction in the literature between male and female adult mortalities, we use $p_m^M = p_m^F$.

The last two columns of table 2 give the critical values μ_1 and μ_2 of primary sex ratio that are evaluated from formula (4). Figure 4 shows the dependence of primary sex ratio on incubation temperature together with the temperature intervals leading to extinction-survival systems. It follows that for *C. serpentina* (*E. orbicularis*), hatchling sex ratios as biased as 1 : 99 (1 : 19) can prevent unconditional extinction. This translates into two egg incubation temperature intervals of about 2°C width and a single, about 1°C-wide interval that enable survival of *C. serpentina* and *E. orbicularis*, respectively.

Mate Search Strategies

In nature, many organisms do not mate at random but rely on more or less elaborate mate search strategies. What consequences do they have for population survival and resistance to adverse conditions? To shed more light on this issue, we inspect some consequences of the diffusive movement and active mate search defined above.

Both Males and Females Move Diffusively. Among all combinations of d_M and d_F , the case $d_M = d_F = 1$ deviates most from the SHM (1). On the other hand, the SHM and the IBM with diffusive movement and high enough values of d virtually coincide (de Roos et al. 1991; McCauley et al. 1993). Figure 5 shows a shift of the extinction boundary toward lower population densities; all extinction boundaries corresponding to higher values of d lie in between the one for the SHM and the one for the IBM with $d_M = d_F = 1$.

Both Males and Females Use Active Mate Search Strategy.

Table 2: Demographic data, reproduction and mortality probabilities, and critical values of primary sex ratio for the snapping turtle *Chelydra serpentina* and the European pond turtle *Emys orbicularis*

| Species | Annual adult mortality | Clutches (eggs) | Fraction achieving maturity (~no.) | Critical values | | | |
|----------------------------|------------------------|-----------------|------------------------------------|-----------------|-----------------|---------|---------|
| | | | | p_r | $p_m^M = p_m^F$ | μ_1 | μ_2 |
| <i>Chelydra serpentina</i> | .04 | 1 (30) | .133 (~4) | 1.0 | .01 | .01 | .99 |
| <i>Emys orbicularis</i> | .10 | 2 (6) | .206 (~2.5) | 1.0 | .033 | .05 | .95 |

Simulations show that mutual active mate search lowers extinction thresholds even more. Figure 6 shows an extinction/survival diagram for a population (with the same initial number of males and females) with various perception neighborhoods (equal for both sexes). We note that the minimum viable population size decreases nonlinearly with increasing perception neighborhood.

As the IBM is inherently stochastic, there is always a nonzero probability that a population of any size will become extinct in a finite time. This stochasticity is due to both demography (variation in numbers of births and deaths over various realizations) and environment (variation in spatial distribution of individuals on the lattice over various realizations). For each combination of initial population size and perception neighborhood, we performed 10 simulation runs starting from different “seeds.” While some combinations in figures 6 and 7 gave only extinction (*asterisks*) or survival (*circles*), some led to both extinction and survival within the 10 runs (*squares*): the squares thus estimate the “region of strong demographic stochasticity,” defined here as a range of initial conditions for which the probability of extinction lies in the interval [0.1, 0.9]. Clearly, this probability decreases with increasing initial population size.

Sedentary Males and Actively Searching Females. In many frogs, males are territorial, do not move during the mating period, and attract females by advertisement calls (Duellman and Trueb 1986). We model the immobility of males by the diffusive strategy with $d_M = 0$ and let the distance s_F for females to hear the male calls vary; we use the same initial number of males and females (fig. 7). Two principal changes occur compared to figure 6: the extinction boundary shifts toward higher population sizes, and the region of strong demographic stochasticity extends.

Three generic phases of population dynamics are observed around the region of strong demographic stochasticity (fig. 8). First, starting from a (uniform) random distribution of individuals on the lattice, abundances of both sexes decrease since mortality outnumbers reproductive events. This phase is the real demonstration of

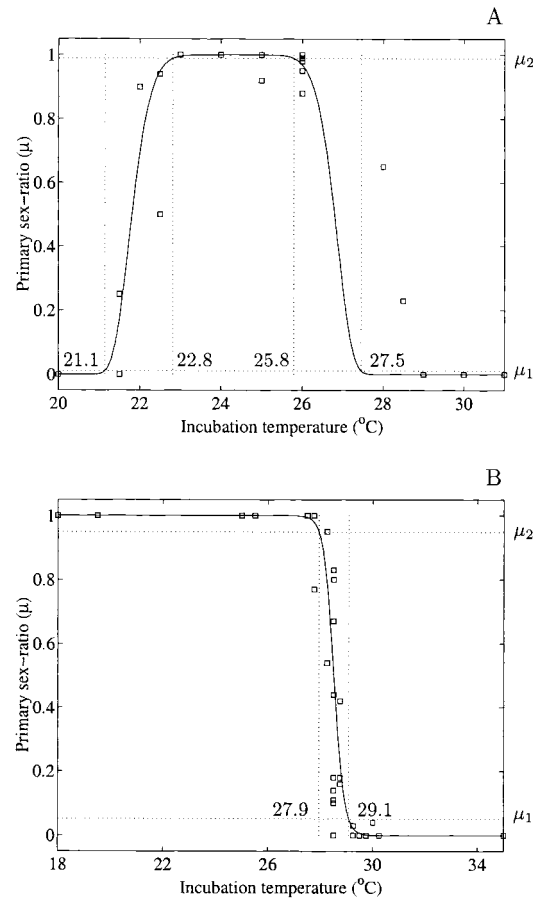


Figure 4: Dependence of primary sex ratio on the egg incubation temperature for the snapping turtle *Chelydra serpentina* (A) and the European pond turtle *Emys orbicularis* (B), combined with primary sex ratio interval (μ_1, μ_2) for which the spatially homogeneous model (eq. [1]) leads to an extinction-survival system. Solid lines denote the best fits of the original data (*squares*) taken from Paukstis and Janzen (1990). Parameter values and data fits: *C. serpentina*: $p_r = 1.0$, $p_m^M = p_m^F = 0.01$, $\mu = \exp[-(t - 24.3)^8/2177.3]$, fitted by the MATLAB procedure “lsqcurvefit”; *E. orbicularis*: $p_r = 1.0$, $p_m^M = p_m^F = 0.033$, $\mu = 1/[1 + \exp[-(28.51 - t)/0.196]]$, taken from Girondot (1999). Values of μ_1 and μ_2 are given in table 2.

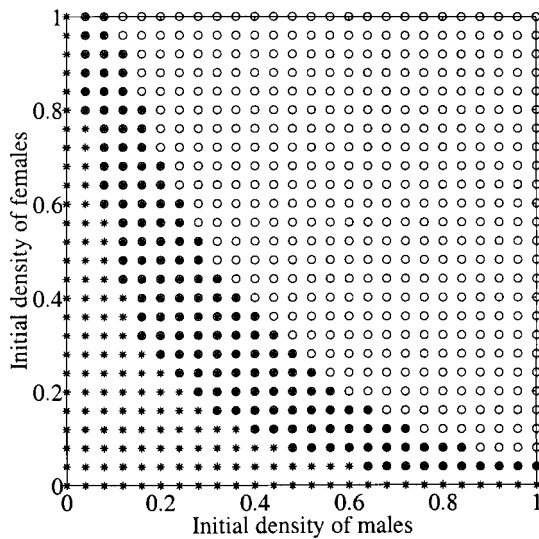


Figure 5: Space of initial male and female population densities divided into the survival (*circles*) and extinction (*asterisks*) parts as determined by the individual-based model (IBM) with diffusive movement, $d_M = d_F = 1$. Circles filled by asterisks show the area where the spatially homogeneous model (eq. [1]) predicts extinction, whereas the IBM with $d_M = d_F = 1$ gives survival. Other parameter values: $\mu = 0.4$, $p_r = 0.1$, $p_m^M = 0.013$, $p_m^F = 0.01$.

scarcity in reproductive possibilities and, if too long, may result in population extinction. During the second phase, males and females start to meet each other with a greater frequency as clusters of individuals begin to form. This increase in pair formation more or less balances mortality and keeps the population relatively constant. Finally, when the clusters become more pronounced, the probability of finding a mate after a recent encounter steadily increases. The population starts to grow, clusters expand radially and fill the lattice, and densities approach the saturation level. The first two phases are negligible if initial numbers of both sexes are high.

Discussion

Spatially Homogeneous Models with the Allee Effect

The term “component Allee effect” was coined for a positive relationship between any component of individual fitness and either numbers or density of conspecifics (Stephens et al. 1999). When experienced at the total fitness level, such a relationship is denoted as a demographic Allee effect by Stephens et al. (1999). In models of population dynamics, the demographic Allee effect is manifested by a reduction of the per capita growth rate at low sizes/densities, usually resulting in negative growth rates and an ultimate extinction.

Some one-dimensional models of the Allee effect are rather artificial (Lewis and Kareiva 1993; Amarasekare 1998a, 1998b). In others (Volterra 1938; Jacobs 1984; Hopf and Hopf 1985; Dennis 1989; Fauvergue et al. 1995; Pfister and Bradbury 1996; Veit and Lewis 1996; Wells et al. 1998), mechanisms reducing individual fitness in small populations are biologically motivated, and the latter models share the following behavior: the origin is always locally stable and populations with too low initial densities become extinct. If mortality is sufficiently small relative to reproduction, two additional equilibria appear. The smaller equilibrium represents a critical density under which the population dies out and above which it attains a saturation level determined by the larger equilibrium.

The two-sex SHM that we developed resembles this behavior; the stability results can be concisely described in terms of compound parameters A_M and A_F that relate the birth and death processes in the population (fig. 1). However, it differs from one-dimensional models in several important aspects. The extinction boundary has a nonlinear (hyperbolic) shape (fig. 2), and predictions of population extinction given by the one- and two-dimensional models are contradictory for some initial male and female population densities (fig. 3). Unlike the one-dimensional descriptions, our model allows adult sex ratio to vary in time and to depend on primary sex ratio, demographic parameters, and initial densities of both sexes. Finally, all the mentioned one-dimensional models include parameters whose estimation from available data may be complicated while our model requires only basic demographic characteristics that are comparatively easy to evaluate.

Populations of reptiles exhibiting TSD would perish in one generation under persistent incubation temperatures that produce only one sex (Janzen 1994). We apply our SHM to assess the combined influence of TSD and the mate-finding Allee effect on long-term survival of the

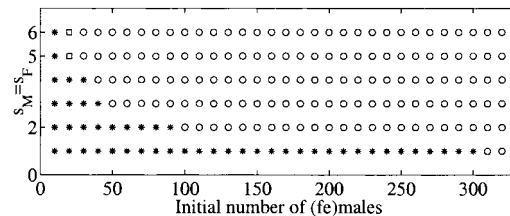


Figure 6: Division of space formed by the initial population size and the perception neighborhood into the survival (*circles*) and extinction (*asterisks*) parts as determined by the individual-based model with active mate-search strategy. Squares show the region of strong demographic stochasticity where at least one out of 10 simulation repetitions leads to survival and at least one leads to extinction. Other parameter values: $\mu = 0.4$, $p_r = 0.1$, $p_m^M = 0.013$, $p_m^F = 0.01$.

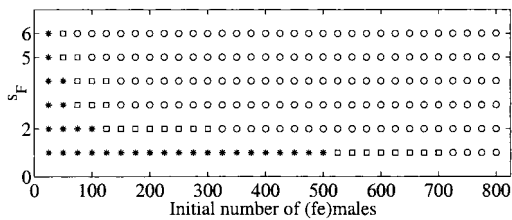


Figure 7: Division of space formed by the initial population size and the perception neighborhood of females into the survival (*circles*) and extinction (*asterisks*) parts as determined by the individual-based model with sedentary males ($d_M = 0$) and actively searching females. Squares show the region of strong demographic stochasticity where at least one out of 10 simulation repetitions leads to survival and at least one leads to extinction. Other parameter values: $\mu = 0.4$, $p_t = 0.1$, $p_m^M = 0.013$, $p_m^F = 0.01$.

snapping turtle *Chelydra serpentina* and the European pond turtle *Emys orbicularis*. This is not intended to give reliable quantitative predictions but to illustrate the potential strategic use of models developed in this article. The fundamental message is that the Allee effect further narrows temperature ranges under which survival is possible. However, knowledge of appropriate spatial and temporal scales, mate search strategies, variations in the egg incubation temperature between nesting sites and years, and further life cycle details of the studied species would be instrumental in adopting any control measures.

Effects of Mate Search

Many organisms are sedentary or move slowly relative to the size of their environment. In addition, individuals need not mate randomly. To reinforce the findings of the SHM, we inspect consequences of two mate search strategies within the spatially explicit IBM: diffusive movement and active mate search. In this aspect, the IBM complements the findings of the spatially homogeneous two-sex models (i.e., models with random mating) introduced by Caswell and Weeks (1986), Lindström and Kokko (1998), and Legendre et al. (1999). These models investigate the effect of various mating systems (ranging from strict monogamy to full polygyny) on population dynamics and do not incorporate the Allee effect; our model keeps a fixed-mating system (monogamous with no fidelity) and focuses on the role of mate search strategies.

We show that the initial abundances of males and females sufficient for the population survival may decrease significantly when changing the mate search strategy from random mating to diffusive movement of both sexes to one actively searching sex to both sexes active (figs. 5–7). The extinction boundary preserves its hyperbolic shape; its shift toward the origin may be explained as follows. If

random mating is replaced by diffusive movement, successful pair formation enhances mating probability of the paired individuals in the next time step due to cluster formation. The probability that a successfully mated individual encounters the same or another partner (e.g., a recent newborn) at the next time step increases—for the same population sizes—with decreasing diffusion range and is higher than the probability x_M/S (x_F/S) of encountering a male (female) in the SHM. Hence, the increase in pair formation compensates for mortality in at least some populations that become extinct according to the SHM. If at least one sex uses active mate search, the formation of successfully breeding clusters is further enhanced by the ability of individuals to effectively find their mates. If both sexes actively search for partners, an individual without a partner may incidentally approach an individual of the opposite sex that still has the possibility to move and mate with it at the same time step. On the other hand, if the other sex is sedentary, they cannot mate before the next time step. This results in a narrower region of strong demographic stochasticity and lower extinction thresholds if both sexes use active search compared to the case where males are sedentary and females active. Under any of the studied strategies, the observations are not qualitatively affected by the use of a larger (256×256) lattice.

If one or both sexes actively search for mates, an increased perception neighborhood facilitates population survival. Using an example with equal initial abundances of both sexes, we show that the extinction threshold is more or less inversely dependent on the perception neighborhood (figs. 6, 7). This result agrees well with predictions of the reaction-diffusion model of a sexually reproducing population studied by Hopper and Roush (1993). Indirect experimental evidence of this dependence is provided by Kindvall et al. (1998) in their field study of the bush cricket *Metrioptera roeseli*. They found that the crickets tend to move more at lower population densities and thus probably increase the effective perception neighborhood. Such behavior could be an adaptive response of organisms to alleviate or avoid the Allee effect at low population sizes or densities.

Both reaction-diffusion models and observations of real populations suggest that the Allee effect leads to a slower rate of spread and growth of populations in early stages of the invasion or (re)introduction, which is followed by a rapid expansion in the environment (Hopper and Roush 1993; Lewis and Kareiva 1993; Kot et al. 1996; Veit and Lewis 1996). We observed similar behavior in IBM simulations. Before successful establishment, populations starting at lower densities invariably passed through three successive stages (fig. 8). Their knowledge may help to better understand mechanisms regulating the spread or extinction of natural populations. Also, it emphasizes dif-

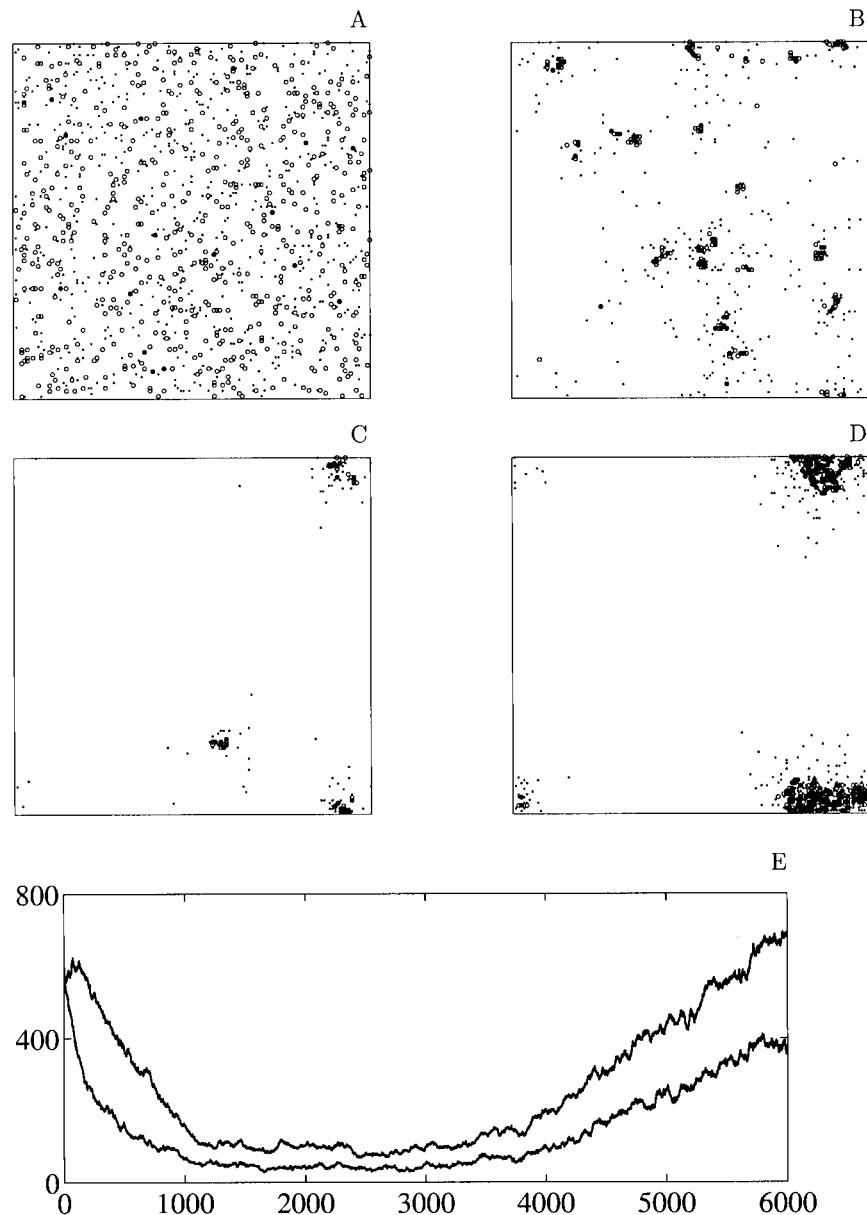


Figure 8: Typical spatiotemporal dynamics of the individual-based model around the region of strong demographic stochasticity: spatial pattern of males (*empty circles*) and females (*filled circles*) at times 0 (A), 500 (B), 2,000 (C), and 5,000 (D), and corresponding temporal evolution (E; *lower curve* = number of males, *upper curve* = number of females). Parameter values: sedentary males ($d_M = 0$); actively searching females ($s_F = 1$); $\mu = 0.4$, $p_r = 0.1$, $p_m^M = 0.013$, $p_m^F = 0.01$.

ferences between local and global densities and shows the importance of scale when assessing the Allee effect.

Although genetic inbreeding may arise as a result of cluster formation and shift extinction boundaries to higher population sizes, behaviors aimed at inbreeding avoidance can also depress population viability. For example, we show in this article that an increase in the rate of diffusive

movement negatively affects the extinction boundary. Also, populations of cooperative breeders may lose by adopting an inbreeding avoidance strategy (Koenig et al. 1999). On the other hand, an increase in the movement rate of actively searching individuals effectively enlarges their perception neighborhood and may shift extinction boundaries to lower population sizes (figs. 6, 7). The take-

home message is that in real populations, many component Allee effects combine to form the overall demographic Allee effect, which determines the ultimate fate of the population (Stephens et al. 1999). However, potential consequences of the component Allee effects should initially be studied separately to understand the underlying mechanisms.

The IBM focuses on consequences of mate search strategies on the strength of mate-finding Allee effect, and is rather simple in its reproduction and mortality rules. Yet, we think this modeling framework is sufficient to get significant insights into the changes that occur when one strategy is replaced by another. The study of additional effects of more realistic reproduction (such as wider dispersal of offspring, time for gathering resources to reproduce, longer maturation time) and mortality (such as the increase in mortality with mating or diffusion) scenarios is beyond the scope of this article. In view of the cluster formation process (fig. 8), we can anticipate at least some qualitative changes. Any additional component of mortality prolongs the first cluster formation phase and pushes populations to lower sizes. Any of the reproduction scenarios listed above dilutes the clusters (gathering of resources and longer maturation time are accompanied by

movement), and the probability of pair formation decreases. All these factors may shift the extinction boundary to higher population densities for any fixed mate search strategy. However, the "ordering" of extinction boundaries in the male-female state space would not change, that is, their distance from the origin would increase in the following order of mate search strategies: both sexes active, one sex active and one moving diffusively, both sexes diffusive, and random mating. The assessment of the changes of distances between these boundaries requires rigorous modeling and simulations.

Acknowledgments

We thank V. Křivan and particularly E. Grist for comments on earlier versions of the manuscript. The manuscript was improved substantially by the suggestions of L. Fahrig, P. Stephens, J. Travis, and two anonymous referees. We acknowledge the financial support of the grants 201/98/P202 (L.B.) and 201/98/0227 (D.S.B.) of the Grant Agency of the Czech Republic. The stay of D.S.B. and L.B. at the Faculty of Biological Sciences was supported by grants VS96086 and MSM123100004 of the Ministry of Education of the Czech Republic.

APPENDIX A

Derivation of the Spatially Homogeneous Model

The SHM (1) is derived under the assumption that individuals are uniformly randomly distributed on a sufficiently large lattice at each time step. Adult individuals may die and/or reproduce. The probability of survival of a male to the next time step is $1 - p_m^M$; hence, the fraction of males that survive to the next time step approaches $1 - p_m^M$ for the lattice size S tending to infinity and the male density x_M/S kept constant. Reproduction and mortality are independent events due to their concurrent ordering. There are $S - x_M$ male-free sites at the beginning of time step. The probability that a male offspring is placed to a particular male-free site from a given nearest neighbor equals the probability that the neighbor contains both adult male and female ($x_M/S \times x_F/S$) times the probability that the pair gives birth to a male offspring ($\mu \times p_r$) times the probability that this offspring is placed to the male-free site ($1/4$). Reproductive events from various neighbors are independent; hence, the probability that the male-free site remains empty at the end of time step is

$$\left(1 - \mu \frac{x_M}{S} \frac{x_F}{S} \frac{p_r}{4}\right)^4.$$

The fraction of male-free sites that is occupied by males at the next time step thus tends to

$$\left[1 - \left(1 - \mu \frac{x_M}{S} \frac{x_F}{S} \frac{p_r}{4}\right)^4\right]$$

for S going to infinity. Analogous expressions hold for females. The mean number of males (x'_M) and females (x'_F) at the next time step may thus be approximated as

$$x'_M = x_M(1 - p_m^M) + (S - x_M) \left[1 - \left(1 - \mu \frac{x_M x_F p_r}{S S 4} \right)^4 \right],$$

$$x'_F = x_F(1 - p_m^F) + (S - x_F) \left\{ 1 - \left[1 - (1 - \mu) \frac{x_F x_M p_r}{S S 4} \right]^4 \right\}.$$

Taking into account that $(1 - w)^4 \approx 1 - 4w$ for a sufficiently small number w and rescaling $x_{M(F)}$ (numbers) to $x_{M(F)}/S$ (densities), we get

$$x'_M = x_M(1 - p_m^M) + \mu p_r x_M x_F (1 - x_M),$$

$$x'_F = x_F(1 - p_m^F) + (1 - \mu) p_r x_F x_M (1 - x_F),$$

which guarantees $0 \leq x'_M, x'_F \leq 1$ provided that x_M and x_F satisfy the same constraint. The neglected higher-order terms become significant only when the population approaches its saturation level. As we are interested primarily in effects that act at lower population densities, it is sufficient to analyze the latter model.

APPENDIX B

Analysis of the Spatially Homogeneous Model

The eigenvalues of the SHM (1) linearized at E^0 are $\lambda_1 = 1 - p_m^M$ and $\lambda_2 = 1 - p_m^F$, and E^0 is thus locally asymptotically stable.

Two distinct nontrivial equilibria,

$$E^u = \begin{pmatrix} x_M^u \\ x_F^u \end{pmatrix} = \begin{pmatrix} \frac{1}{2}(1 - A_M + A_F - \sqrt{D}) \\ \frac{1}{2}(1 + A_M - A_F - \sqrt{D}) \end{pmatrix},$$

$$E^s = \begin{pmatrix} x_M^s \\ x_F^s \end{pmatrix} = \begin{pmatrix} \frac{1}{2}(1 - A_M + A_F + \sqrt{D}) \\ \frac{1}{2}(1 + A_M - A_F + \sqrt{D}) \end{pmatrix}$$

occur if, and only if, $\sqrt{D} \equiv \sqrt{(1 - A_M + A_F)^2 - 4A_F} > 0 \Leftrightarrow \sqrt{A_M} + \sqrt{A_M} < 1$.

The distance $d(E^s, E^u) = \sqrt{D}$ of E^s from E^u decreases with increasing A_M and A_F :

$$\frac{\partial(d(E^s, E^u))}{\partial A_F} = \frac{-1 - A_M + A_F}{\sqrt{D}} < 0 \text{ for all } A_F < (1 - \sqrt{A_M})^2,$$

$$\frac{\partial(d(E^s, E^u))}{\partial A_M} = \frac{-1 + A_M - A_F}{\sqrt{D}} < 0 \text{ for all } A_M < (1 - \sqrt{A_F})^2,$$

The distance $d(E^0, E^u) = \sqrt{1 - A_M - A_F + (A_M - A_F)^2 - \sqrt{D}}$ of E^0 from E^u increases with increasing A_M and A_F due to $0 < \sqrt{D} < \min\{1 - A_M, 1 - A_F\} < 1$:

$$\frac{\partial(d(E^0, E^u))}{\partial A_M} = \frac{(1 - A_M + A_F)(1 - \sqrt{D}) + \sqrt{D}(A_M - A_F)}{2d(E^0, E^u)\sqrt{D}} > 0 \text{ for all } A_M < (1 - \sqrt{A_F})^2,$$

$$\frac{\partial(d(E^0, E^u))}{\partial A_F} = \frac{(1 + A_M - A_F)(1 - \sqrt{D}) + \sqrt{D}(A_F - A_M)}{2d(E^0, E^u)\sqrt{D}} > 0 \text{ for all } A_F < (1 - \sqrt{A_M})^2.$$

The singular case of one nontrivial equilibrium $E^* = (x_M^*, x_F^*) = (1 - \sqrt{A_M}, \sqrt{A_M})$ occurs if, and only if, $D = 0 \Leftrightarrow \sqrt{A_M} + \sqrt{A_F} = 1$. It is structurally unstable and thus biologically irrelevant.

APPENDIX C

The Role of Primary Sex Ratio

The sum $\sqrt{A_M} + \sqrt{A_F}$ is a convex function of μ as $\partial^2(\sqrt{A_M} + \sqrt{A_F})/\partial\mu^2 > 0$. Moreover, $\sqrt{A_M} + \sqrt{A_F} \rightarrow +\infty$ for $\mu \rightarrow 0$ or 1. The sum attains its global minimum

$$\min_{0 < \mu < 1} (\sqrt{A_M} + \sqrt{A_F}) = \left(\frac{\sqrt[3]{p_m^M} + \sqrt[3]{p_m^F}}{\sqrt[3]{p_r}} \right)^{3/2}$$

at

$$\mu = \mu^* = \frac{p_m^M - \sqrt[3]{(p_m^M)^2 p_m^F} + \sqrt[3]{p_m^M (p_m^F)^2}}{p_m^M + p_m^F}.$$

If the inequality (3) holds, then primary sex ratios $\mu_1 < \mu^* < \mu_2$ exist such that $\sqrt{A_M} + \sqrt{A_F} = 1$ for $\mu = \mu_1$ and $\mu = \mu_2$. The SHM (1) possesses two distinct nontrivial equilibria for $\mu_1 < \mu < \mu_2$, one nontrivial equilibrium for $\mu \equiv \mu_1$ and $\mu = \mu_2$, and only the trivial equilibrium E^0 for $\mu < \mu_1$ or $\mu > \mu_2$. The SHM (1) is extinction-doomed ($\sqrt{A_M} + \sqrt{A_F} > 1$) for all μ if the inequality (2) holds. It is also extinction-doomed for all μ if $\sqrt[3]{p_m^M} + \sqrt[3]{p_m^F} \equiv \sqrt[3]{p_r}$, except for the singular case $\mu = \mu^*$. In that case, the SHM (1) possesses one nontrivial equilibrium due to $\sqrt{A_M} + \sqrt{A_F} = 1$ and is structurally unstable.

Solving the equality $\sqrt{A_M} + \sqrt{A_F} = 1$ with respect to μ in the special case $p_m^M = p_m^F$, we get the formula (4); the distance $\mu_2 - \mu_1 = \sqrt{1 - 4P - 8P^2 - 8P\sqrt{P(1 + P)}}$ increases with decreasing ratio $P \equiv p_m^M/p_r$ because

$$\frac{\partial(\mu_2 - \mu_1)}{\partial P} = - \frac{2 \left[\sqrt{1 + P(1 + 4P)} + \sqrt{P(3 + 4P)} \right]}{(\mu_2 - \mu_1)\sqrt{1 + P}} < 0.$$

Literature Cited

- Amarasekare, P. 1998a. Allee effects in metapopulation dynamics. *American Naturalist* 152:298–302.
- . 1998b. Interactions between local dynamics and dispersal: insights from single species models. *Theoretical Population Biology* 53:44–59.
- Asmussen, M. A. 1979. Density-dependent selection. II. The Allee effect. *American Naturalist* 114:796–809.
- Caswell, H., and D. E. Weeks. 1986. Two-sex models: chaos, extinction, and other dynamic consequences of sex. *American Naturalist* 128:707–735.
- Charnov, E. L., and J. Bull. 1977. When is sex environmentally determined? *Nature (London)* 266:828–830.
- Christiansen, J. L., and R. R. Burken. 1979. Growth and maturity of the snapping turtle (*Chelydra serpentina*) in Iowa. *Herpetologica* 35:261–266.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999a. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* 14:405–410.
- Courchamp, F., B. Grenfell, and T. Clutton-Brock. 1999b. Population dynamics of obligate cooperators. *Proceedings of the Royal Society of London B, Biological Sciences* 266:557–563.

- Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling* 3:481–538.
- de Roos, A. M., E. McCauley, and W. G. Wilson. 1991. Mobility versus density-limited predator-prey dynamics on different scales. *Proceedings of the Royal Society of London B, Biological Sciences* 246:117–122.
- Duellman, W. E., and L. Trueb. 1986. *Biology of amphibians*. McGraw-Hill, New York.
- Ehrlich, P. R., and J. Roughgarden. 1987. *The science of ecology*. Macmillan, New York.
- Fahse, L., C. Wissel, and V. Grimm. 1998. Reconciling classical and individual-based approaches in theoretical population ecology: a protocol for extracting population parameters from individual-based models. *American Naturalist* 152:838–852.
- Fauvergue, X., K. R. Hopper, and M. F. Antolin. 1995. Mate finding via a trail sex pheromone by a parasitoid wasp. *Proceedings of the National Academy of Sciences of the USA* 92:900–904.
- Girondot, M. 1999. Statistical description of temperature-dependent sex determination using maximum likelihood. *Evolutionary Ecology Research* 1:479–486.
- Girondot, M., and C. Pieau. 1993. Effects of sexual differences of age at maturity and survival on population sex ratio. *Evolutionary Ecology* 7:645–650.
- Groom, M. J. 1998. Allee effects limit population viability of an annual plant. *American Naturalist* 151:487–496.
- Hopf, F. A., and F. W. Hopf. 1985. The role of the Allee effect in species packing. *Theoretical Population Biology* 27:27–50.
- 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.
- Iverson, J. B. 1991. Pattern of survivorship in turtles (order Testudines). *Canadian Journal of Zoology* 69:385–391.
- Jacobs, J. 1984. Cooperation, optimal density and low density thresholds: yet another modification of the logistic model. *Oecologia (Berlin)* 64:389–395.
- Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences of the USA* 91:7487–7490.
- Janzen, F. J., and G. L. Paukstis. 1991. Environmental sex determination in reptiles: ecology, evolution, and experimental design. *Quarterly Review of Biology* 66:149–179.
- Kear, J., and A. J. Berger. 1980. The Hawaiian goose: an experiment in conservation. Buteo, Vermillion, S.D.
- Keeling, M. 1999. Spatial models of interacting populations. Pages 64–99 *in* J. M. McGlade, ed. *Advanced ecological theory*. Blackwell Science, Oxford.
- Kindvall, O., K. Vessby, A. Berggren, and G. Hartman. 1998. Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roseli*: an experimental study. *Oikos* 81:449–457.
- Koenig, W. D., M. T. Stanback, and J. Haydock. 1999. Demographic consequences of incest avoidance in the cooperatively breeding acorn woodpecker. *Animal Behaviour* 57:1287–1293.
- Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Legendre, S., J. Clobert, A. P. Møller, and G. Sorci. 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* 153:449–463.
- Levitan, D. R., M. A. Sewell, and F. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248–254.
- Lewis, M. A., and P. Kareiva. 1993. Allee dynamics and the spread of invading organisms. *Theoretical Population Biology* 43:141–158.
- Lindström, J., and H. Kokko. 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proceedings of the Royal Society of London B, Biological Sciences* 265:483–488.
- Lynch, M., J. Conery, and R. Bürger. 1995. Mutation accumulation and the extinction of small populations. *American Naturalist* 146:489–518.
- McCauley, E., W. G. Wilson, and A. M. de Roos. 1993. Dynamics of age-structured and spatially structured predator-prey interactions: individual-based models and population-level formulations. *American Naturalist* 142:412–442.
- McGlade, J. M. 1999. Individual-based models in ecology. Pages 1–22 *in* J. M. McGlade, ed. *Advanced ecological theory*. Blackwell Science, Oxford.
- Murray, J. D. 1990. *Mathematical biology*. Springer, Berlin.
- Obst, F. J. 1986. *Turtles, tortoises and terrapins*. Edition, Leipzig.
- Paukstis, G. L., and F. J. Janzen. 1990. Sex determination in reptiles: summary of effects of constant temperatures of incubation on sex ratios of offspring. *Smithsonian Herpetological Information Service* 83:1–28.
- Pfister, C. A., and A. Bradbury. 1996. Harvesting red sea urchin: recent effects and future predictions. *Ecological Applications* 6:298–310.
- Sæther, B. E., T. H. Ringsby, and E. Røskoft. 1996. Life history variation, population processes and priorities in

- species conservation: towards a reunion of research paradigms. *Oikos* 77:217–226.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution* 14:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* 87:185–190.
- 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.
- Volterra, V. 1938. Population growth, equilibria, and extinction under specified breeding conditions: a development and extension of the logistic curve. *Human Biology* 3:3–11.
- Wells, H., E. G. Strauss, M. A. Rutter, and P. H. Wells. 1998. Mate location, population growth and species extinction. *Biological Conservation* 86:317–324.

Associate Editor: Lenore Fahrig