



Single-species Models of the Allee Effect: Extinction Boundaries, Sex Ratios and Mate Encounters

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We critically review and classify models of single-species population dynamics subject to the demographic Allee effect with emphasis on non-spatial, deterministic approach. Inclusion of spatial movement and stochastic phenomena does not substantially change the behaviour; stochasticity only “blurs” step-like character of the Allee effect into a sigmoidal form. The outcome of all non-spatial, deterministic models is either unconditional extinction, extinction-survival scenario (ES), or unconditional survival. Three major model classes are recognized: (1) one-dimensional heuristic models, (2) one-dimensional models with mating probability and fixed sex ratio, and (3) two-sex models with variable adult sex ratio. Each class is characterized by the shape of extinction boundary which separates extinction from survival in the ES scenario. The latter two classes may give better predictions of extinction thresholds than heuristic models but require specific information and are data intensive. In one-dimensional models with fixed sex ratio, population cannot survive if density/number of males decreases below some threshold while there is no such restriction on females. Individual-based models seem to be most capable of explaining mechanisms leading to the Allee effect.

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1. Introduction

Warder C. Allee brought attention to the possibility of a positive relationship between (components of) individual fitness and population size more than 50 years ago. Since then, it has been widely recognized that individuals of many species benefit from the presence of conspecifics. The phenomenon, broadly referred to as the Allee effect, attracted a lot of attention

during the last decade with the rise of conservation biology. Based on a widespread evidence in natural populations, several mechanisms have been hypothesized to invoke the Allee effect; Dennis (1989), Courchamp *et al.* (1999a), Stephens & Sutherland (1999) and Møller & Legendre (2001) provide thorough reviews. All mechanisms share the absence of cooperation at low population sizes (Odum & Allee, 1954; Philip, 1957). By far, the most cited and obvious cause of the Allee effect is the difficulty of finding mates at low population sizes in sexually reproducing species. The necessity of a minimal group size to rear offspring, search for food and/or sustain predator attacks is less frequently mentioned.

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Population-dynamic consequences of the Allee effect are of primary importance in conservation biology and other fields of ecology. However, models incorporating the Allee effect are fairly diverse and scattered in the literature, which may lead to confusion and reduce the utility of the Allee effect concept. We also believe that this phenomenon deserves a more systematic approach, given the increased attention it has now been receiving. The purpose of this article is thus two-fold: (1) to review and classify the ways used to introduce the Allee effect, and (2) to provide a condensed introduction and a critical list of models that have been used to quantify it. We focus mainly on the most often used approach: non-spatial and deterministic descriptions of a single-species population, which are based on ordinary differential or difference equations. We divide them into distinct classes and look at the population-dynamic behaviour of each class, using the shape of an extinction boundary in the male–female state space (Berec *et al.*, 2001) as an important intrinsic characteristic. As the Allee effect usually acts at low population sizes, the role of stochasticity (and space) is also briefly discussed. A thorough treatment of the Allee effect in stochastic populations has been prepared by Dennis (2002).

The terminology involved in the Allee effect classification is still somewhat controversial (see Discussion). In this review, we adopt the definition proposed by Stephens *et al.* (1999) that embraces the original concept of Odum & Allee (1954): the (component) Allee effect is a positive relationship between any measurable component of individual fitness and population size, quantified by the number or density of conspecifics. When manifested at the total fitness level, the relationship is referred to as the demographic Allee effect. Odum & Allee (1954) were apparently the first in this context who regarded per capita growth rate of the population as a proxy for the total fitness.

In fisheries science, the Allee effect is often discussed in close relation to depensation (Myers *et al.*, 1995; Frank & Brickman, 2000; Jennings, 2001, and others). However, depensation refers to lower than expected spawner-recruitment relationships (Jennings, 2001) and is usually quantified by departures from the Beverton-Holt

or Ricker spawner-recruitment functions. It is principally a population-level phenomenon that may have little in common with the Allee effect (Stephens *et al.*, 1999); for this reason, we do not include models of depensation in this review.

In virtually all models known to us, the demographic Allee effect is manifested by a reduction in the per capita growth rate at low population sizes. However, the demographic Allee effect may also affect populations of larger sizes (Stephens *et al.*, 1999). In what follows, we use only “the Allee effect” instead of “the demographic Allee effect” for the sake of brevity.

2. Models

Many papers investigating single-species population dynamics that exhibit the Allee effect are based on simple heuristic (phenomenological), non-spatial and deterministic models. These models, reviewed in Section 2.1, do not provide any detailed insight into the underlying biology. Other models, reviewed in Sections 2.2 and 2.3, have been developed on the basis of plausible, biologically motivated mechanistic rules. Curiously enough, almost all these models known to us are *one-dimensional* but rely heavily on the mechanism that involves *two sexes*: the difficulty in finding mates at low population sizes. It is true that these models apply more generally to processes which are enhanced by the encounter of conspecifics, but the link is more or less phenomenological. All “mechanistic” explanations known to us are concerned with mate shortage. Models that discern between the sexes are treated in Section 2.3.

2.1. HEURISTIC APPROACH

The essence of this approach goes back at least to Odum & Allee (1954): the expected or observed density-dependent per capita growth rate is fitted by a suitable function. Here, we consider a single population whose growth in a homogeneous environment is described either by the ordinary differential equation (\dot{N} stands for the time derivative of N throughout the article)

$$\dot{N} = Ng(N) \quad (1)$$

or, in the case of non-overlapping generations, by the difference equation

$$N_{k+1} - N_k = N_k g(N_k). \quad (2)$$

In both cases, $N_{[k]}$ is the population size (number or density) and the function $g(N_{[k]})$ denotes the density-dependent per capita growth rate, which is negative/positive for decreasing/growing populations. We concentrate on cases where the demographic Allee effect takes place at low population sizes; examples of the Allee effect at larger sizes—in the sense of Stephens *et al.* (1999) Fig. 2(d)—are very limited [see Kokko and Sutherland (2001) and Section 3.2.3 in Discussion]. The per capita growth rate describing the Allee effect at low population sizes is “hump-shaped”: its maximum is attained at $N_{[k]} = N_{max} > 0$. Below this “optimal” population size, positive effects of the presence of conspecifics prevail and $g(N_{[k]})$ is increasing, while negative density dependence dominates and $g(N_{[k]})$ is therefore decreasing above it. Most models include crowding effects and prevent indefinite growth by assuming $g(N_{[k]}) < 0$ for sufficiently large $N_{[k]}$. These characteristics are summarized in Fig. 1. For the purpose of stability analysis, the per capita growth rate g should “behave nicely” (in mathematical language, it should be sufficiently smooth near the equilibria and continuous elsewhere), which is true for all models proposed so far. In the difference equation (2), it should also satisfy $g(N_k) \geq -1$ for $N_k > 0$ to assure nonnegative population sizes.

2.1.1. Possible Outcomes

In one-dimensional heuristic models (1) and (2), three basic scenarios corresponding to Fig. 1 may occur:

Unconditional extinction (UE)—if the (demographic) Allee effect is too strong, g is negative for all $N_{[k]}$ and populations go inevitably extinct regardless of their initial size;

Extinction–survival (ES)—at moderate levels of the Allee effect, g is positive for intermediate values but negative for very low or high values of $N_{[k]}$. Two equilibria emerge; the lower one, denoted E^u , is unstable and the higher E^s is

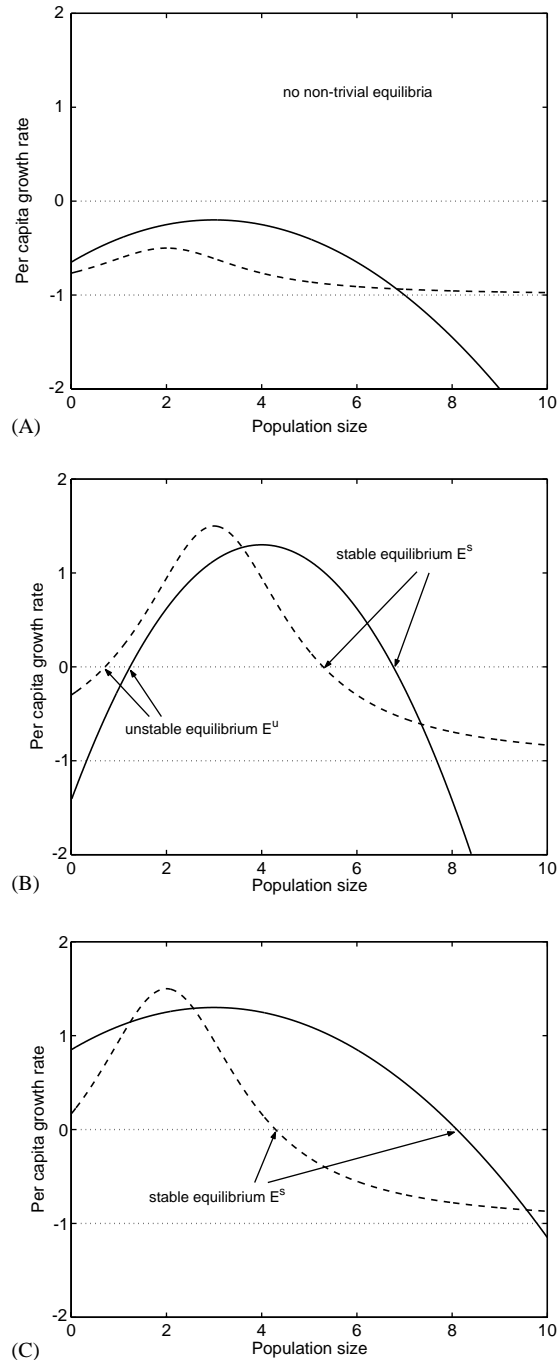


FIG. 1. Three types of per capita growth rate $g(N_{[k]})$ corresponding to three basic population dynamic scenarios: (a) UE; $g(N_{[k]})$ is always negative, (b) ES; $g(N_{[k]})$ intersects zero at two points, and (c) US; $g(N_{[k]})$ intersects zero at one point. (—) shows behaviour of a continuous-time model while (- - -) represents a discrete-time model. The curves are plots of functions (3) and (9) with appropriate parameter values.

locally stable. The origin E^0 is locally stable; populations starting below E^u go extinct while those starting above E^u establish at E^s ;

Unconditional survival (establishment) (US)—by weakening the influence of the Allee effect further, the unstable equilibrium E^u vanishes, E^0 becomes unstable as the per capita growth rate g is positive for all $N_{[k]} > 0$, and all populations establish at E^s even though their per capita growth rate at low sizes is still increasing with $N_{[k]}$.

The ES scenario is the most familiar consequence of the Allee effect, and the difference between extinction and establishment is what we are most frequently interested in practice.

In addition to these three scenarios, E^s may be destabilized in discrete-time models if the decrease of g at E^s is too steep ($g'(E^s) < -1$), giving rise to cyclic behaviour or chaotic phenomena in very much the same way as the discrete logistic equation does (May, 1974). We do not consider special and biologically irrelevant cases such as the appearance of one semistable equilibrium on the edge of UE and ES scenarios.

2.1.2. Fine Tuning

The reviewed heuristic models are summarized in Table 1.

The (negative) quadratic polynomial (3) is an obvious candidate that possibly describes the per capita growth rate under the Allee effect. Models (4) and (5) are its variants, and are obtained by modifying the well-known Verhulst logistic model by introducing another threshold $A < K$. The scenarios that may be fitted indicate their flexibility (more detailed analysis of the models' capabilities is beyond the scope of this review and we refer the reader mainly to the original papers).

Model (6) merits more detailed discussion. It is an appealing choice since the dynamics approaches logistic growth for large N , but it has been considered only with $C = 0$ so far. In that case, we should “define” $Ng(N) := 0$ for $N = 0$ to make the origin E^0 an equilibrium. More importantly, $g(N)$ approaches $-\infty$ for $N \rightarrow 0$ and $A > 0$, which imposes higher extinction rates on small populations than in all other models in this section. This fact is not crucial in the basic single-species model but its role in more

complicated settings has never been discussed properly. On the other hand, model (6) has already been used in competition, predation and metapopulation models by Courchamp *et al.* (2000) and Brassil (2001). We therefore propose to consider model (6) with $C > 0$ which fixes both objections and in fact yields a more flexible model with variable extinction rates. Indeed, model (6) with $C = r/K$ gives the same per capita growth rates as model (7) after reparameterization.

Model (8) proposed by Jacobs (1984) combines, to some extent, features of heuristic approach with biological reasoning. It treats the Allee effect and negative density dependence separately and may combine them in a wide range of biologically plausible relationships; on the other hand, the model is quite complicated.

The “hyperbolic” model (9) and “logistic” model (13) allow for all three scenarios. However, models (12) and (13) give negative population sizes for large N_k and may thus be used only for description of reasonably small populations. The Ricker-type model (11) appeared in several formulations: Avilés (1999) used it with $c = r/K$ and Asmussen (1979) discussed this model with $\gamma = 1$, $c = 1/T$ and $r = 1 + \ln(G/T)$. Although such reparameterizations will generally have a profound impact on the way each parameter affects the model, they are marginal to our purposes.

An alternative approach to eqns (1) and (2) has been proposed by Scheuring (1999) who used a discrete-time model

$$N_{k+1} = rN_k a(N_k) f(N_k). \quad (14)$$

In this setting, $a(N_k)$ is a mathematical construct that captures the Allee effect while $rf(N_k)$ models the negative density dependence: $a(0) \geq 0$, $a'(N) > 0$ for all $N > 0$ and $\lim_{N \rightarrow \infty} a(N) = 1$; $f(0) > 0$, $f'(N) < 0$ for all $N > 0$ and $0 < \lim_{N \rightarrow \infty} rf(N) < 1$. In general, this model could fit observed dynamics by choosing appropriate functional forms of $a(N_k)$ and $f(N_k)$, and could even describe the case in which the component Allee effect is not translated in the demographic Allee effect. Model (6) in fact provides an example of (14) in the continuous-time framework.

TABLE 1

Reviewed one-dimensional heuristic models of single-species population dynamics subject to the Allee effect, with possible scenario outcomes

Model	Per capita growth rate	Parameter constraints	Scenarios [conditions]	References
(3)	$g(N) = r - b(N - a)^2$	$a, b > 0$	UE, ES, US	Edelstein-Keshet (1988)
(4)	$g(N) = r \left(1 - \frac{N}{K}\right) \left(\frac{N}{K} - \frac{A}{K}\right)$	$r, K > 0$	ES [$A > 0$], US [$A \leq 0$]*	Lewis & Kareiva (1993), Amarasekare (1998a) Amarasekare (1998b), Keitt <i>et al.</i> (2001)
(5)	$g(N) = r \left(1 - \frac{N}{K}\right) \left(\frac{N}{A} - 1\right)$	$r, K, A > 0$	ES	Gruntfest <i>et al.</i> (1997), Courchamp <i>et al.</i> (1999a)
(6)	$g(N) = r \left(1 - \frac{N}{K}\right) \left(1 - \frac{A + C}{N + C}\right)$	$r, K, C > 0$	ES [$A > 0$], US [$A \leq 0, C > A $]*	Wilson & Bossert (1971), Courchamp <i>et al.</i> (1999b) Courchamp <i>et al.</i> (2000), Brassil (2001), all for $C = 0$
(7)	$g(N) = b + \frac{a - N}{1 + cN} N$	$a, c > 0$	UE/ES [$b < 0$]*, US [$b \geq 0$]	Takeuchi (1996)
(8)	$g(N) = r_0 + uw \frac{N^w}{N^w + v} - cN^z$	$u, v, w, c, z > 0$	UE, ES, US	Jacobs (1984)
(9)	$1 + g(N_k) = \frac{Gb}{(N_k - T)^2 + b}$	$b, T, G > 0$	UE [$G < 1$]*, ES/US [$G > 1$]	Asmussen (1979)
(10)	$1 + g(N_k) = \frac{\rho N_k}{A + N_k^2}$	$\rho, A > 0$	UE [$\rho < 2\sqrt{A}$], ES [$\rho > 2\sqrt{A}$]	Hoppensteadt (1982), Jacobs (1984)
(11)	$1 + g(N_k) = N_k^\gamma \exp(r - cN_k)$	$r, c > 0, 1 \geq \gamma > 0$	UE [$e^r < (ec/\gamma)^\gamma$], ES [$e^r > (ec/\gamma)^\gamma$]	Asmussen (1979), Avilés (1999)
(12)	$1 + g(N_k) = N_k^\gamma r \left(1 - \frac{N_k}{K}\right)$	$r, K > 0, 1 \geq \gamma > 0$	UE $\left[r < \frac{(1 + \gamma)^{1+\gamma}}{(K\gamma)^\gamma}\right]$, ES	Avilés (1999)
(13)	$1 + g(N_k) = N_k^\gamma + r \left(1 - \frac{N_k}{K}\right)$	$r, K > 0, 1 > \gamma > 0$	$\left[r > \frac{(1 + \gamma)^{1+\gamma}}{(K\gamma)^\gamma}\right]$ UE/ES [$r < 1$], US [$r > 1$]	Avilés (1999)

Note: Conditions on parameters in square brackets are given only in simple cases; asterisks denote cases not considered in the cited papers. Note that a cyclic behaviour and chaos in discrete-time models with the ES and US scenarios may occur. See the text for more comments on model (6).

2.1.3. *Biological Rationale*

Although the heuristic models focus mainly on population-dynamic consequences of the Allee effect and disregard its actual causes, we should ask whether biologically plausible explanations may support them, and what are the limiting assumptions. The “basic” quadratic per capita growth rate (3) traces back to Volterra (1938) and suggests a population with constant per capita mortality, encounters based on bimolecular collisions (i.e. proportional to N^2), and linearly decreasing birth rate (or linearly decreasing probability of offspring survival) in crowded habitats: $\dot{N} = -\mu N + \lambda(N)N^2$, $\lambda(N) = \lambda\alpha - \gamma N$; see Dennis (1989). This interpretation implies negative and thus biologically meaningless values of the birth rate λ for large N . It could be amended by setting $\lambda(N) = 0$ for $N^* > (\lambda\alpha)/\gamma$ which would correspond to zero offspring production or absolute offspring mortality in populations beyond N^* . Quadratic per capita growth rate also arises in quadratic contact processes (Durrett, 1999) as a spatially homogeneous limit of the following individual-based model (IBM): the environment is a regular lattice composed of identical square sites; time runs continuously; each lattice site is occupied with at most one individual; occupied sites become vacant at rate d and vacant sites become occupied at rate $bk/4$, where k is the number of diagonally adjacent pairs of occupied neighbours. The corresponding mean-field approximation (i.e. the spatially homogeneous limit of the IBM) reads:

$$\dot{v} = -dv + b(1-v)v^2, \quad (15)$$

with v being the density of occupied lattice sites. This is exactly model (3) with $a = 1/2$ and $r = -d + b/4$. In biological terms, model (15) describes e.g. non-selfing hermaphrodites or asexual obligate cooperators that need one helper to rear the offspring. Durrett & Levin (1994) also formulated a discrete-time version of the underlying individual-based model.

Another plausible explanation of an Allee-type growth rate of a population is, surprisingly, provided by a predator–prey model: we may consider a prey population that grows logistically in the absence of predators and a constant

predator population C with Holling type II functional response; see also Dennis & Patil (1984), Dennis (1989) and references therein. The resulting equation (e scales the predator encounter rate of prey and a models predator saturation)

$$\dot{N} = rN(1 - N/K) - eCN/(a + N) \quad (16)$$

is formally identical with a model including mate shortage (see below).

2.2. INCLUSION OF MATING PROBABILITY

A significant group of one-dimensional models modifies a “non-Allee” population dynamics by multiplying birth terms by the probability $P(N)$ that a female finds and mates with at least one male during the reproductive period. This probability is of interest when one mating is sufficient for the female to realize full reproductive potential, and is a function of male population size. All models treated in this section require that the proportion μ of males in the population is constant (at least during the reproductive period, but could in principle vary between generations) and assume that mating is promiscuous with no mate choice. Many situations are reasonably characterized by $P(N)$ that satisfies three basic criteria:

- (i) no mating occurs at zero population size,
- (ii) probability of mating (monotonically) increases with increasing population size,
- (iii) mating is (almost) guaranteed in very large/dense populations.

Mathematically, these criteria translate to $P(0) = 0$, $P'(N) > 0$ and $\lim_{N \rightarrow \infty} P(N) = 1$, respectively. Three forms satisfying (i)–(iii) have been used in the literature most frequently:

$$P(N) = 1 - \exp(-\beta N),$$

Negative exponential (NE),

after Dennis (1989), (17)

$$P(N) = N/(N + \theta),$$

rectangular hyperbolic (RH),

after Dennis (1989), (18)

$$P(N) = 1 - (1 - a)^{cN},$$

power complement (PC), (19)

with $\beta, \theta, c > 0$ and $1 > a > 0$. Dennis (1989) and McCarthy (1997b) fitted forms (17) and (18) to different data sets and obtained only small differences in the resulting functional forms. Probability form (19) is technically identical with form (17) as easily shown by substituting $\beta = -c \ln(1 - a)$.

2.2.1. Biological Rationale

The biological rationale behind all three forms has received considerable attention. The NE form (17) was discussed a number of times (Philip, 1957; Klomp *et al.*, 1964; Kuno, 1978; Dennis, 1989; Hopper & Roush, 1993; McCarthy, 1997a) and its motivation goes back to early models of insect parasitism (Nicholson & Bailey, 1935). One plausible derivation requires Poisson- and independently distributed males in space at each time instant and constant density of available males during the reproductive period (see Appendix A). The latter assumption is met, for example, in polygynous systems with negligible mortality during the reproductive period. The Poisson-type assumptions were considerably weakened by alternative derivations of Dennis (1989).

Sometimes it is more appropriate to consider the distance l traversed by females during the reproductive period or the effective search area S visited by the females during that period as a random variable (Dennis, 1989; McCarthy, 1997a). Dennis (1989) showed that for exponentially distributed S with mean D , the mean probability that a female mates successfully becomes the RH form (18) with $\theta = 1/(\mu D)$. He further assumed gamma and Raleigh distributions for S and derived even more complicated formulas for $P(N)$; in general, he showed that any continuous, density-independent distribution of S leads to concave [“concave down” in the terminology of Dennis (2002)] shape of the probability $P(N)$.

Alternative derivation of the RH form (18) involves “competition for mates”, which seems to have been anticipated in the first succinct

formulation of the RH form as a mating function by Kostitzin (1940). Based on this line of argument, the RH form has been used for years as a model of the mating probability of the sterile male release method in insect pest control, see Dennis (1989). More recently, McCarthy (1997a) derived the RH form with $\theta = 2/S$ by assuming 1:1 sex ratio ($\mu = 0.5$) and a monogamous mating system in which females compete for mates; the number/density of available males declines as individual females succeed to mate. For a biased sex ratio ($\mu \neq 0.5$), one may get (McCarthy, 1997a,b)

$$P(N) = \frac{\mu(\exp[(2\mu - 1)NS] - 1)}{\mu(\exp[(2\mu - 1)NS] + 1) - 1}. \quad (20)$$

In this case, the basic assumption (iii) has to be relaxed (see Appendix A); due to mate competition and monogamy, all females cannot mate if they outnumber males regardless of the population size N . The monogamous mating system was also considered by Wells and his collaborators. They chose a slightly phenomenological approach, did not explicitly consider the effective search area S and instead focused on individual “meeting rates”. For 1:1 sex ratio, they derived the RH form (18) with $\theta = 2/(2\alpha\tau)$ where α scales the meeting rate of randomly moving individuals, a is the probability of mating success given that a male–female meeting occurred, and τ is the length of the reproductive period (Wells *et al.*, 1998). For a biased sex ratio, they derived form (20) with S formally replaced by $2\alpha\tau$ (Wells *et al.*, 1990).

Stephan & Wissel (1994), Wells *et al.* (1998) and Grevstad (1999) used the PC form (19). It assumes that a female mates with a male upon encounter with a fixed probability a and that the (mean) number of meetings a female has with males during the reproductive period is proportional to μN . The proportionality constant equals S provided that the male distribution is Poisson and independent at each time instant (see above). A female mates at least once (with any male) with probability $1 - (1 - a)^{\mu SN}$ if the encounters are independent.

Kuno (1978) used yet another approach and studied cases in which males search for females.

He arrived at the PC form (19) with $a = S/S_T$ corresponding to the searching efficiency (area S covered by each male during the mating period is divided by the total habitat size S_T) and $c = \mu S_T$ if N is the population density. He also remarked that the NE form (17) with $\beta = \mu S$ approximates (in the limit) the previous form for a very large habitat size; note that this case coincides with Philip's formula (see Appendix A) if males and females reverse their roles and $S = 2\epsilon l$. Kuno further discussed the effect of restricted male and/or female capacity of mating frequency and obtained similar shapes of mating probability functions.

Møller & Legendre (2001) focused on differential reproductive success of females with respect to male phenotypes or male attractiveness: natural observations show that females often refrain from reproduction or reproduce at low rates if only "unattractive" males are available. For the case of monogamous pair formation and the mean sex ratio $\mu = 0.5$, they composed three models that relate population size to the female mating probability: the first one with non-differential reproductive success of females, the second one assuming genetic incompatibility of two male and female phenotypes forming the population, and the third one with mating preferences of females given by male attractiveness (each female chooses a male with a fixed probability upon encounter). All these models give probabilistic curves with properties (i)–(iii).

Last but not least, the NE and RH forms also emerge in the context of mating frequency (Dennis, 1989). This fact is important in species whose fecundity increases with the number of matings. In particular, this phenomenon has been observed in flour beetles that have been extensively used in early Allee effect studies in 1930s, see for example Park (1933).

2.2.2. Possible Outcomes

Once we have obtained the probability $P(N)$ that an individual female mates during the reproductive period, we have to find an appropriate way to plug this term in population dynamics. In closed populations with no immigration, the net change in numbers/density is a result of birth and death processes. It seems

natural to multiply the birth term $B(N)$ by $P(N)$ as the limitation in mating possibilities affects reproduction. Therefore, in continuous-time case,

$$\begin{aligned}\dot{N} &= P(N)B(N) - D(N) \\ &= [B(N) - D(N)] - B(N)[1 - P(N)] \\ &= G(N) - B(N)[1 - P(N)],\end{aligned}\quad (21)$$

whereas in discrete-time case,

$$\begin{aligned}N_{k+1} - N_k &= P(N_k)B(N_k) - D(N_k) \\ &= [B(N_k) - D(N_k)] - B(N_k)[1 - P(N_k)] \\ &= G(N_k) - B(N_k)[1 - P(N_k)].\end{aligned}\quad (22)$$

Here, $D(N_{[k]})$ is the death term and $G(N_{[k]})$ is the growth function in the absence of the mate-finding Allee effect (that is, when all females always mate). Various growth and birth functions G and B and probability terms P found in the literature are summarized in Table 2.

The first four models in Table 2 do not include saturation at high population sizes and lack the upper stable equilibrium E^s (populations either go extinct or explode). On the other hand, Hopf & Hopf (1985) and Wang *et al.* (1999) were the only ones who included logistics in the birth term, which is perhaps more appropriate for describing crowding effects. Also, observe that the US scenario can never be achieved if the probability form $P(N)$ in models (21) and (22) satisfies assumption (i); on the contrary, the hyperbolic-shaped probability form used by Hopf & Hopf (1985) is positive even at zero population density ($\gamma > 0$) and thus also admits the US scenario.

Mating probabilities (17)–(20) depend in many instances on the (fixed) sex ratio μ . We have already mentioned several typical examples:

Mating probability (17)

$$\text{with } \beta = 2\epsilon l\mu \text{ or } \beta = \mu S,$$

Mating probability (18) with $\theta = 1/(\mu D)$,

Mating probability (19) with $c = \mu S$,

Mating probability (20). (23)

TABLE 2
Growth and birth functions, probability forms and possible scenario outcomes in reviewed models

$G(N_{[k]})$	$B(N_{[k]})$	$P(N_{[k]})$	Scenarios	References
$(b - d)N$	bN	NE form	ES†	Dennis (1989)
$(b - d)N$	bN	RH form	ES†	Dennis (1989), Gyllenberg <i>et al.</i> (1999)
$(b - d)N$	bN	PC form	ES†	Wells <i>et al.</i> (1998)
$(b - d)N_k$	bN_k	RH form	ES†	Wells <i>et al.</i> (1998)
$rN(1 - N/K)$	bN	NE form	UE/ES	Philip (1957)
$rN(1 - N/K)$	bN	RH form	UE/ES	Dennis (1989), Stephens & Sutherland (1999)
$(b - d)N(1 - N/K)$	bN	PC form	UE/ES	Wells <i>et al.</i> (1998)
$bN(1 - N/R) - dN$	$bN(1 - N/R)$	RH form	UE/ES	Wang <i>et al.</i> (1999)
$bN(1 - N/R) - dN$	$bN(1 - N/R)$	$\frac{\gamma N_0 + N}{N_0 + N}$	UE/ES [$b\gamma < d$], US [$b\gamma > d$]	Hopf & Hopf (1985)

Note: Parameters $b, d, r, K, R, \gamma, N_0$ are assumed positive and $b > d$ wherever both of them occur. Absence of the upper equilibrium (no saturation) is marked by a dagger.

It turns out that all proposed forms are increasing functions of μ for any fixed population size N (see Appendix B). How does this dependence translate into population dynamics? All models cited in Table 2 include the ES scenario. We may thus plot the unstable equilibrium E^u as a function of μ for each $1 > \mu > 0$ in the male–female state space; their ensemble forms the extinction boundary sensu Berec *et al.* (2001) in models (21) and (22). The shape of the extinction boundary in models (21) and (22) with saturation shares important characteristics irrespective of the mating probability, growth and death terms used (Fig. 2). The boundary has everywhere a positive slope and is characterized by one or two important points, E^{**} and usually also E^* , in all models in Table 2 (see Appendix B). The point E^* corresponds to a minimum sex ratio μ_{min} below which the population always goes extinct regardless of its initial size; it is absent in models that lack saturation and include mating probabilities (17)–(19). There is also a minimal size of male population E^{**} below which the population dies out regardless of female number/density but no such minimal female population exists provided there are enough males.

2.2.3. Atypical Inclusion of the Allee Effect

Several models do not fit formulas (21) and (22). Burgman *et al.* (1993) did not differentiate

between birth and death terms and combined the Ricker model with the RH probability form (18):

$$N_{k+1} = N_k e^{r-\beta N_k} \left(\frac{N_k}{A + N_k} \right), \quad (24)$$

this model can be either seen as an example of Scheuring’s approach (14) or, though artificially, rewritten as formula (22) with $P(N_k) = N_k / (A + N_k)$, $B(N_k) = N_k e^{r-\beta N_k}$ and $D(N_k) = N_k$ by subtracting N_k from both sides of the equation.

Veit & Lewis (1996) modelled population dynamics of birds experiencing a pair formation process and a limited availability of nesting sites and got the following difference equation:

$$N_{k+1} = sN_k + \frac{cN_k^2}{4/\tau\sigma + 2N_k + N_k^2/\delta}, \quad (25)$$

where s denotes the probability of survival to the next year, c is the average number of one pair offspring surviving the summer, τ is the length of pair formation (i.e. reproductive) period, σ is the rate at which pairs are formed, and δ is the finite density of nests. This model assumes random mate search by both sexes and 1 : 1 sex ratio; it allows the ES scenario if $c/(1 - s) > 2(1 + \sqrt{4/(\sigma\tau\delta)})$ and the UE scenario (reverse inequality).

So far, we have mentioned only one-dimensional models. Models that treat sexes separately are discussed in the next section. Beddington (1974) offered an example that incorporates the

Allee effect into a heuristic projection matrix model. He considered density-dependent coefficients in the Leslie matrix that were fitted to empirical data; the fit yielded a “hump-shaped” fecundity function and gave rise to a non-zero unstable population equilibrium.

Essentially the same approach was adopted by Pfister & Bradbury (1996), who developed a simple, discrete-time, three-size class model of red sea urchin population dynamics,

$$\begin{aligned} N_{1,k+1} &= s_1(1 - g_1)N_{1,k} + i_1N_{1,k}, \\ N_{2,k+1} &= s_1g_1N_{1,k} + s_2(1 - g_2)N_{2,k} + i_2N_{2,k}, \\ N_{3,k+1} &= s_2g_2N_{2,k} + s_3N_{3,k} + i_3N_{3,k} \end{aligned} \quad (26)$$

with s_j being the fraction that survives to the next time step in each size class j , g_j the fraction that grows to the next size class, and i_j the immigration rate. Any new recruitment is included in the $i_1N_{1,k}$ term. Empirical studies (Levitan *et al.*, 1992) suggest that in red sea urchins low population density of adults is related to either decreased fertilization success or decreased abundance of juveniles. Therefore, Pfister & Bradbury modelled both i_1 and s_1 as the increasing function of total adult density $N_2 + N_3$,

$$\phi(1 - \exp(-\beta(N_2 + N_3))), \quad \phi, \beta > 0,$$

which is related to the NE form (17). Model (26) lacks saturation and apparently admits only the ES scenario for a wide range of parameter values (the US scenario arises only in biologically implausible situations); numerical simulations reveal a hyperbolic-like extinction boundary in the (N_1, N_2, N_3) state space.

2.3. SPATIAL APPROACH AND INDEPENDENT SEXES

More specific models of the Allee effect using spatial and/or two-sex approach seem to be scarce. Although important *per se*, we do not consider here metapopulation studies which describe the Allee effect within local patches using one-dimensional heuristic models and only combine them with between-patch migration (Amarasekare, 1998a; Gyllenberg *et al.*, 1999; Brassil, 2001; Gruntfest *et al.*, 1997; Courchamp

et al., 2000). We are thus left with only a few models which treat the sexes separately and are characterized by a variable adult sex ratio (= proportion of males in the population) in contrast with a fixed primary sex ratio (= proportion of males in the offspring).

Hopper & Roush (1993) studied the spread of small invading populations using a two-sex reaction–diffusion equation. The essence of their results is captured also by the reaction part of the model:

$$\begin{aligned} \dot{M} &= \mu_p b P(M) F + b_a (1 - P(M)) F - dM, \\ \dot{F} &= (1 - \mu_p) b P(M) F - dF, \end{aligned} \quad (27)$$

where M and F are male and female subpopulations, respectively, and μ_p is the primary sex ratio. The probability $P(M)$ takes the NE form (17) with M instead of N , and β equals the effective search area S . The interesting term $b_a(1 - P(M))F$ is due to arrhenotoky (virgin females produce purely male offspring), a phenomenon observed in some haplodiploids; setting $b_a = 0$ disables it for other species. Hsu & Fredrickson (1975) described population dynamics of two-sex population with age structure and “promiscuous/monogamous” mating systems. In the simplest case (“promiscuous” mating, age-independent processes), they obtained model (27) with $b_a = 0$ and a complicated functional form equivalent to the product $bP(M)$, in which the function $P(M)$, nevertheless, satisfies “probability-of-mating” assumptions (i)–(iii).

The approach developed by Berec *et al.* (2001) employs an IBM with discrete space and time. The mean-field difference equations are written as

$$\begin{aligned} M_{k+1} - M_k &= \mu_p p_r M_k F_k (1 - M_k) - p_m^M M_k, \\ F_{k+1} - F_k &= (1 - \mu_p) p_r F_k M_k (1 - F_k) - p_m^F F_k, \end{aligned} \quad (28)$$

where $1 \geq M_k$ ($F_k \geq 0$) are male (female) densities at time k , p_m^M (p_m^F) is the probability that a male (female) does not survive to the next time step, p_r is the probability of producing one offspring upon pair formation and μ_p is the primary sex ratio.

Both models accommodate only the UE and ES scenarios and are characterized by a hyperbolic-shaped extinction boundary in the male–female state space in the ES scenario [Fig. 2(a); see also Berec *et al.* (2001), Fig. 2]. However, solutions starting above the extinction boundary grow indefinitely and do not approach any saturation value in model (27); inclusion of radial diffusion conserves this behaviour. The exact location of the boundary depends on population demography (primary sex ratio, reproduction and mortality rates/probabilities) in both models and, moreover, on the adopted mate-search strategies (random mixing, diffusive movement, active search for mates) in the IBM counterpart of model (28).

Recently, Stephens *et al.* (2002) described population dynamics of alpine marmots. They presented four models of different complexities, which included six stage classes and were parameterized by field data. All four models demonstrated the Allee effect at low population sizes (ES and US scenarios).

2.4. STOCHASTIC PHENOMENA

Dennis (1989) examined the role of demographic stochasticity in comparison with deterministic predictions. In his formulation of discrete birth–death processes, population size is treated as a discrete variable and individual births and deaths are modelled directly as stochastic events; a birth in the population during a short time interval Δt is assumed to occur with the probability

$$P[N(t + \Delta t) = n + 1 | N(t) = n] = \lambda(N)\Delta t,$$

while the probability of death during Δt increases linearly with population size:

$$P[N(t + \Delta t) = n - 1 | N(t) = n] = \mu N \Delta t.$$

The probability that two or more events occur within Δt is assumed negligible. Under these assumptions, Dennis (1989) computed the probability of population extinction for $\lambda(N) = \lambda NP(N)$, with $P(N)$ given by forms (17) and (18). He showed that this probability is a sigmoidally decreasing function of the initial population size and proved that its inflection

point corresponds to the unstable equilibrium of the deterministic models. “Blurring” of the step-like character of the Allee effect in deterministic models into a sigmoidal form in stochastic models has also been observed in computer simulations performed by Berec *et al.* (2001).

Dennis (1989) claimed that at larger population sizes, environmental stochasticity is better captured by continuous-time stochastic processes formulated by means of stochastic differential equations of the type

$$dN(t) = N(t)g(N(t)) dt + \sigma N(t) dW(t), \quad (29)$$

where $W(t)$ is a Wiener process. In this set-up, the critical population size caused by the Allee effect manifests itself both as an inflection point in the probability of never attaining an upper population size before attaining a low one, and as a minimum (= antimode) of the corresponding stationary probability density function if such a function exists. Dennis exemplified the latter statement for the models listed in the fifth and sixth rows of Table 2 and the quadratic per capita growth rate (3) of Table 1. He also concluded that the multiplicative noise $\sigma N(t) dW(t)$ magnifies the effect of limited mating and thus exacerbates the Allee effect. For high noise levels σ^2 , the stationary probability distribution ceases to exist and the population faces certain extinction even if the initial population size is above the lower equilibrium of the deterministic model counterpart $\dot{N} = Ng(N)$.

Dennis (2002) stated that many different types of stochastic models (including discrete birth–death processes) can often be approximated by diffusion processes. One way to describe such processes is to compute the approximate increment dN_t of the population size N_t from time t to time $t + dt$ as

$$dN_t = m(N_t) dt + \sqrt{v(N_t)} dW_t,$$

where dW_t has a normal distribution with zero mean and a variance of dt . The infinitesimal mean $m(N)$ specifies the underlying deterministic tendencies, while the infinitesimal variance $v(N)$ corresponds to stochastic fluctuations. The effects of demographic stochasticity

generally give rise to $v(N) = \alpha N$, $\alpha > 0$, while the effects of environmental stochasticity can be approximated by $v(N) = \beta N^2$, $\beta > 0$ (Engen *et al.*, 1998). Both types of stochasticity can be combined into $v(N) = \alpha N + \beta N^2$. Using the first passage probability (i.e. probability that a population starting at N reaches a given lower size before a given upper one), Dennis (2002) showed that an inflection point in this probability represents a type of stochastic equilibrium. These equilibria satisfy $m(N) = 0$ and do not depend on $v(N)$. Consequently, the Allee effect is only carried over from the deterministic part to the entire stochastic equation: the critical population size E^u of the deterministic model marks the inflection point in the first passage probability in the stochastic version (Dennis, 2002). Below the inflection point, extinction is guaranteed or at least disproportionately enhanced.

3. Discussion

3.1. ALLEE EFFECT IN THEORETICAL AND APPLIED ECOLOGY

Various mechanisms such as the need of a minimal group size necessary to successfully raise offspring, produce seeds, forage, and/or sustain predator attacks, or enhanced genetic inbreeding at low population sizes have been proposed as potential sources of the Allee effect (Jacobs, 1984; Lamont *et al.*, 1993; Saether *et al.*, 1996; Courchamp *et al.*, 1999a; Stephens & Sutherland, 1999). However, the most cited potential source of the Allee effect is doubtlessly the difficulty in finding mates in small/sparse, sexually reproducing populations (Ehrlich & Roughgarden, 1987; Levitan *et al.*, 1992; Groom, 1998; Kindvall *et al.*, 1998; Wells *et al.*, 1998, and others).

The Allee effect, modelled at the level of a single local population, may propagate into and profoundly affect dynamic consequences of the whole community or ensemble of local populations. This has been demonstrated for the rate of spread of invading populations (Lewis & Kareiva, 1993; Kot *et al.*, 1996; Veit & Lewis, 1996; Berec *et al.*, 2001; Wang *et al.*, 2002), optimal distance of dispersal (South & Kenward, 2001), invasion pinning (Keitt *et al.*, 2001), persistence

and size heterogeneity of metapopulations (Gruntfest *et al.*, 1997; Amarasekare, 1998a; Gyllenberg *et al.*, 1999; Brassil, 2001), and stability of competing populations (Wang *et al.*, 1999).

The possible role of the Allee effect in evolutionary biology has been suggested by Hopf & Hopf (1985), who discussed its importance in species packing along a continuous resource axis. Some authors (Mosimann, 1958; Kuno, 1978; Wells *et al.*, 1998, and others) argued that selection for adaptations which increase probability of mate encounters has shaped the evolution of dioecious species. On the other hand, Møller & Legendre (2001) suggested that sexual selection ("choosiness") is an important factor giving rise to the Allee effect. Avilés (1999) interpreted some heuristic models in the light of social group size dynamics; she suggested that dynamic instability (oscillations and chaos) could result in the take-over of selection among the highly integrated social groups as the primary evolutionary force. Asmussen (1979) studied density-dependent natural selection via a one-locus-two-allele model where the fitness of a genotype was assumed to be an Allee-type function of the total population size.

Last but not least, the Allee effect may shape predictions in many conservation issues. It was shown to affect optimal release strategies of biological control agents (Hopper & Roush, 1993; Grevstad, 1999). For example, the data on the release of exotic birds in Australia and New Zealand (Green, 1997) clearly support the idea of minimum viable population, linked to the ES scenario under the Allee effect. Dennis (1989) theoretically supported the practical use of the Allee effect in pest control via releases of sterile males. The role of the Allee effect in harvested populations and, vice versa, profound effects of harvesting on populations subject to the Allee effect was emphasized e.g. by Dennis (1989), Levitan & Young (1995), Pfister & Bradbury (1996), Claereboudt (1999), Stephens & Sutherland (1999) and Lundquist (2000). It was supported by field studies of marine invertebrates (Pfister & Bradbury, 1996; Stoner & Ray-Culp, 2000) and reviewed by Levitan & Sewell (1998). Kokko & Sutherland (2001)

showed that “ecological traps” in changing environments (i.e. malassessment of changing habitats) may create a behaviourally mediated Allee effect at larger population sizes and concluded that this phenomenon should be included in habitat management.

3.2. MODEL CATEGORIES

Although the previous subsection is only a condensed list of various implications of the Allee effect, it clearly illustrates how ubiquitous and universally recognized the Allee effect has recently become. On the other hand, a quick overview of the literature reveals that many papers draw their (often general) conclusions from deliberately selected models. However, to which extent does a particular model choice contribute to the conclusions reached? This question is often neglected. In the following discussion, we attempt to clarify relationships between the models that were used so far and indicate their strong points and weaknesses.

In general, the reviewed models fall into three basic categories:

- one-dimensional heuristic models mimicking density-dependent per capita growth rate by an appropriately chosen function,
- one-dimensional models that include a mating probability term and assume a fixed sex ratio, and
- models with separately treated sexes and variable adult sex ratio.

In our opinion, basic criteria for model assessment should include at least its ability to cover the desired (or observed) extinction/survival scenario and, it should describe the shortage of mates in more detail, the way it models relations between the sexes. The latter characteristic is closely linked to the shape of the extinction boundary. It turns out that differences between the three model classes are exemplified in the modelling approach as well as in the shape of the extinction boundary. The flexibility of each model with respect to possible scenarios is mostly due to the selection of the birth and death terms.

3.2.1. *Extinction Scenarios and Extinction Boundary*

Three possible scenarios—unconditional extinction (UE), extinction or survival depending on the initial conditions (ES), and unconditional survival or establishment (US)—are typical for all single-species models demonstrating the demographic Allee effect. Some models fit only one or two of these; discrete-time models with the ES and US scenario may also exhibit cyclic and chaotic behaviour. Although the role of parameters differs among the models, the order of the US, ES and UE scenarios generally follows with increasing mortality and/or decreasing reproduction.

As this review shows, most known models can be divided into three large model classes, each with a very different background. It is therefore not *a priori* clear on which grounds these classes should be compared. Detecting the shape and position of the extinction boundary (which separates initial conditions leading to establishment and extinction in the ES scenario) is perhaps the most important application of such models in conservation biology, pest control, and invasion studies. The most cited mechanism leading to the Allee effect is the shortage of mates in sexually reproducing populations, and we thus propose to examine the extinction boundary in the male–female state space (Fig. 2). Examination of the extinction boundary position as a function of parameters for so many diverse models is far beyond the limits of this paper. Instead, we focus only on the relation between its shape and the model used.

In two-sex models, location and meaning of the extinction boundary is straightforward. The boundary is hyperbolic-shaped because these models treat the sexes “equally” [Fig. 2(a), line III].

Heuristic models are one-dimensional and we must therefore “divide” the population into males and females to find the extinction boundary. If we artificially split the population into males and females [Fig. 2(a), line I], the boundary is linear with negative slope of -45° . It is a straight line corresponding to a threshold female density if we assume that the dynamics are driven only by females and the present males

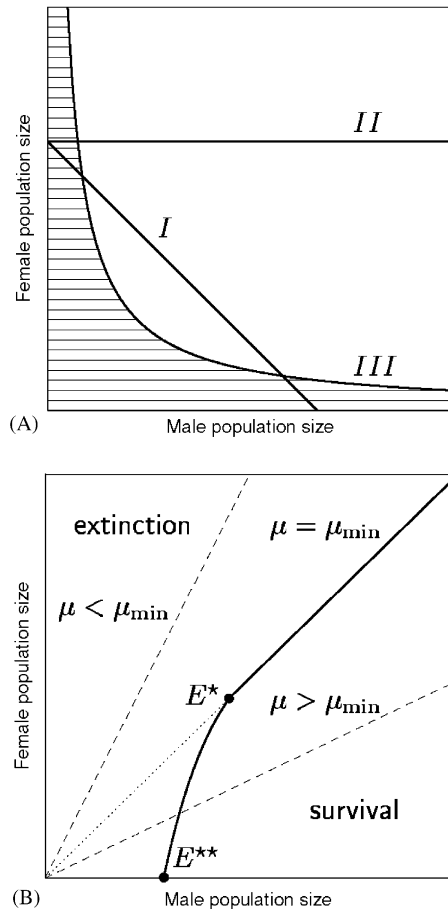


FIG. 2. Diagrammatic representation of the ES scenario in male–female state space for three main model classes. (a) Extinction boundary in one-dimensional heuristic models (lines I and II) and spatial models with variable sex ratio (curve III). Line I connecting points $(0, E^u)$ and $(E^u, 0)$ corresponds to artificial division of the population into males and females. Horizontal line II arises if females drive the dynamics (E^u is the unstable equilibrium of the one-dimensional model). Area of initial male and female population sizes leading to extinction in spatial models with variable sex ratio is indicated by horizontal lines; it is located below line I or II in heuristic models. (b) Extinction boundary (bold) in one-dimensional models including saturation and the probability of female reproductive success. Populations to the right of the boundary survive and to the left become extinct. The boundary is given by the union of all unstable equilibria E^u . E^* corresponds to unstable equilibrium for minimum sex ratio μ_{min} necessary for survival; E^{**} corresponds to unstable equilibrium for sex ratio $\mu \rightarrow 1$. Each radius corresponds to one system with a fixed sex ratio [(- - -) corresponds to $\mu < \mu_{min}$ and $\mu > \mu_{min}$; (....) corresponds to $\mu = \mu_{min}$].

always guarantee full reproduction [Fig. 2(a), line II].

In models based on mate shortage, extinction boundary must again be constructed via

expansion to the full male–female state space by considering all sex ratios $0 < \mu < 1$. For each fixed sex ratio μ , the dynamics would, of course, be restricted to a single radius. The shape and location of the boundary is now determined by the dependence of the lower, unstable equilibrium E^u on the fixed sex ratio μ as explained in Appendix B. Its shape contrasts with the other two model categories dramatically: the extinction boundary is a straight line corresponding to a constant minimal number of males in models that lack saturation, and it is a curve with positive slope in models with upper equilibria. In the latter case, population dies out if there are, somewhat paradoxically, “too few males or too many females” [Fig. 2(b)]. Both shapes of the extinction boundary are surprising and suggest that males may be “at least as important” for survival as females in such situations. However, the marked difference in the role of sexes and unusual model behaviour become more natural if we realize that these models include competition for mates, and mated females drive the reproduction process. These models suggest that conservation studies of species that obey such a behaviour should perhaps be concerned more with the population sex ratio or (surprisingly) male population size than with total or female population size.

3.2.2. Heuristic Approach

In heuristic models (Table 1), the principal advantage is at the same time the main disadvantage: the shortage of mates and other biological mechanisms are only indirectly treated. This class of models focuses on a qualitative description of the expected or observed form of the per capita growth rate, and does not discern between the sexes. These models have been suggested as a reasonable approximation of systems which are asexually reproducing or driven by female dynamics. However, the idea of a population with no or super-abundant mates [corresponding to extinction boundaries I and II in Fig. 2(a)] contradicts the assumption of mate shortage and should be used with caution in this context. Their use in population viability analysis and validation of conservation measures (Boyce, 1992, and others) is debatable.

On the other hand, heuristic models may prove useful in a wide range of situations, especially if the knowledge of life history details and field data are inadequate. They may also be used as a compromise to interpret the consequences of the Allee effect in more complicated model settings. In such “rough-grained” applications, knowledge of the exact shape of the per capita growth rate is often unnecessary. In view of this fact, almost any of the plethora of models presented in Table 1 can be used if it provides the right scenario or fits available data well enough. We thus regard all examined heuristic models as reasonable phenomenological descriptions of the Allee effect, especially if exact mechanisms remain unknown. Models suitable for “general” use should, in our opinion, include at least the ES and US scenarios. Model (8) of Jacobs (1984) is probably the most flexible one but contains many parameters and is strongly nonlinear. Model (6) provides a more-or-less direct transition from the logistic growth to a model with the Allee effect.

3.2.3. *Modelling Mate Shortage*

The fact that the shortage of mates is by far the most cited mechanism leading to the Allee effect is fully reflected in modellers’ approach; a number of models treating reduced mating opportunities at low population sizes have been developed.

What positive and negative features do they have? Despite the obvious drawback of assuming a fixed sex ratio, they represent a more direct approach than heuristic modelling and aim at a more accurate description by including reasonably motivated probabilistic terms. All models in this category are based on biologically plausible mechanisms and include at least the ES scenario; however, models with linear birth and death terms (first four in Table 2) lack upper equilibria and could be used only for the study of small, usually invading populations. All standard mating probability forms assume very low mating probability at low population sizes, and all models in Table 2 (except the last one with a different probability form) thus do not include the US scenario. All probability forms (17)–(20)

describing mate shortage give similar results when fitted to stationary data and simple models of population dynamics (Dennis, 1989; McCarthy, 1997a); our simulations suggest that they also give at least qualitatively similar results in population-dynamic models (21) and (22) summarized in Table 2. Models of sexual selection, developed by Møller & Legendre (2001), as well as models of tick mating (Rohlf, 1969) and models that include restricted male and/or female capacity of mating frequency (Kuno, 1978), also result in similar probability curves and have analogous dynamical consequences. This body of literature indicates that most, if not all, mechanisms involving mate shortage generally lead to mating probability satisfying conditions (i)–(iii) given in Section 2.2. Moreover, the NE probability form (17) was also used to describe the fertilization success in broadcast spawners among marine invertebrates (Pennington, 1985; Denny & Shibata, 1989; Claereboudt, 1999), suggesting further situations under which the “mate encounter” approach may be useful.

Remarkably, there is an interesting link between models involving sexual reproduction and predation: Holling type II functional response and the RH probability form (18) are, apart from scaling, described by the same function. Thus, a simple model (16) involving non-Allee type of inherent prey dynamics and a constant number of predators is formally identical with a model that describes mate shortage (May, 1977; Dennis, 1989). Taking this parallel one step further, the inclusion of Holling type III functional response creates two stable and two unstable equilibria (Ludwig *et al.*, 1978; Murray, 1990). Such a system would thus lead to the manifestation of the Allee effect at larger population sizes in the sense of Stephens *et al.* (1999), Fig. 2(d).

3.2.4. *Modelling Sexes Separately*

The assumption of a constant sex ratio is limiting in many natural populations, for example in species with different life histories of both sexes. It can be relaxed by treating both sexes separately. Quite surprisingly, few such models

include the Allee effect; only two of them explicitly use spatial context. In a reaction–diffusion model of population dispersal by Hopper & Roush (1993), the mate shortage is introduced via the same probability as in the previous model class; it is in fact “cross-bred”. The model used by Berec *et al.* (2001) is based on an individual-based approach and fairly simple, biologically motivated assumptions. The Allee effect is not explicitly incorporated in the model but emerges as a natural consequence of the assumptions.

It should also be noted that two-sex models implicitly assume some particular form of the pairing process (which is hidden in reproduction terms). These models may thus be further generalized by adding explicit dynamics of pairs (Ashih & Wilson, 2001; Boukal, submitted, and others). Obviously, different mating systems and pair formation scenarios require different modelling. This issue will be treated in more detail in a forthcoming paper.

3.3. STOCHASTICITY

Apart from the Allee effect, alternative explanations for small population extinctions include demographic and environmental stochasticity, and their roles have often been discussed (Dennis, 1989; Hopper & Roush, 1993; Stephan & Wissel, 1994; Lande, 1998; Grevstad, 1999; Berec *et al.*, 2001).

The Allee effect definition (Stephens *et al.*, 1999) followed in this paper was partly motivated by Lande (1998), who claimed that demographic stochasticity alone can lead to an Allee-like effect. To achieve this, Lande examined diffusion models of stochastic population dynamics (with both demographic and environmental stochasticity) and transformed them to a scale with isotropic noise. He showed that “a stochastically unstable equilibrium may exist on the new scale, corresponding to a small population size, below which most population trajectories tend to decline toward extinction”. Stephens *et al.* (1999) therefore intended to separate these phenomena from the “real” Allee effect on the basis of density-dependent individual fitness. However, the biological meaning of the transformed scale in Lande’s (1998)

approach is not entirely clear and his results are therefore difficult to interpret.

On the other hand, Dennis (1989, 2002) theoretically demonstrated that the zero–one, step-like extinction probability characteristic of the deterministic models of the Allee effect is “blurred” into a sigmoidally decreasing function of the initial population size if demographic and/or environmental stochasticity is added. The inflection point of such a function corresponds to the unstable equilibrium (threshold) of the deterministic case; populations below the critical size might increase by chance while populations above it might still decrease and possibly go extinct. Other papers on stochastic ODEs predict that the Allee effect is manifested by a local maximum (= mode; corresponding to a carrying capacity) and minimum (= antimode; corresponding to the unstable equilibrium) in the stationary probability density function for population size provided that such a density exists (Dennis & Patil, 1984; Dennis, 1989). Recently, Dennis (2002) showed that the inflection point result holds regardless of the type of stochastic fluctuations for a broad class of models, and he also demonstrated that models containing demographic noise alone do not display this threshold behaviour. Lundquist (2000) obtained similar “blurring” of the Allee effect in a model of the fertilization success in broadcast spawners and Berec *et al.* (2001) observed the same behaviour in an individual-based model of mate search.

These results suggest that the original concept of individual fitness depending on population size (Odum & Allee, 1954) excludes Lande’s (1998) thesis of demographic variability being responsible for some kind of phenomenological Allee effect. It nevertheless seems that extinctions of small populations are governed by intricate relationships among the Allee effect and demographic and environmental stochasticity.

For example, Møller & Legendre (2001) showed theoretically that for any fixed population size, the reproductive success of a female (measured as the probability of being mated) decreases if demographic stochasticity in sex ratio is taken into account. Grevstad (1999) favoured the role of environmental variability and the Allee effect in successful establishment

of small invading populations such as biological control agents, and concluded that demographic stochasticity alone is not the key factor. Finally, Hopper & Roush (1993) suggested that an Allee effect may limit establishment of introduced parasitoids more than environmental stochasticity.

4. Concluding Remarks

1. The three model classes recognized in this review are based on different assumptions and may in fact have radically different uses. Recommendations for practical use in a given situation are thus difficult to draw. Heuristic models provide general, first-step insight into the consequences of the Allee effect, especially if life history details and field data are poorly known. However, their predictive power is low and we argue that they usually cannot provide reliable *a priori* validation of future conservation (manipulative) efforts such as translocation of endangered populations (Griffith *et al.*, 1989). Indeed, at most a few authors have tried to use these models predictively. The other two classes are based on specific mechanisms, require more information and are data intensive. On the other hand, they are predisposed to yield better predictions of minimum viable population size, especially if the model parameters can be directly estimated; examples involving mate shortage were collected for example in Dennis (1989). In particular, we believe that the approach adopted e.g. in Bercé *et al.* (2001) and Stephens *et al.* (2002)—gathering key/relevant life history characteristics of a particular species and transforming them into a model without *a priori* inclusion of the Allee effect—can most efficiently explain the mechanisms invoking the Allee effect, and provide models that are easily applicable in real populations.

2. As the review demonstrates, most non-heuristic models of the Allee effect focus on mate shortage in sexually reproducing species. As already acknowledged by Courchamp *et al.* (2000), adequate and biologically sound models of the Allee effect for other mechanisms still remain to be proposed. Despite the fact that some papers use general terms such as “cooperation and disoperation” (Odum & Allee, 1954),

“sociality” (Philip, 1957) and “cooperative breeding” (Courchamp *et al.*, 1999b; Courchamp *et al.*, 2000, and others), they involve only heuristic models and models based on/inspired by mate shortage. This fact is unsettling: profound differences between model categories emphasize that good understanding of the species’ biology is needed for realistic modelling and its application in conservation measures. Stephens *et al.* (2002) provide a detailed example of such a study.

3. The interplay between the Allee effect and spatial and stochastic phenomena still deserves further study. As shown by Dennis (2002), demographic and environmental stochasticity alone cannot lead to the Allee effect (in its original meaning). On the other hand, various spatially explicit models always predict extinction of sufficiently sparse, sexually reproducing populations. We should therefore look for similar general rules and examine under which conditions stochastic phenomena and/or spatial movement (*viz.*, invasion pinning) lead to the manifestation of the Allee effect.

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Appendix A

Probability forms (17) and (20)

The following derivation of probability form (17) is largely taken from Philip (1957). Denoting the distance of mate detection in the direction perpendicular to direction of movement as ε and recalling that N is the total population density, it follows that a searching female does not encounter any mate during a short step of length Δl with a probability equal to the zeroth term of the Poisson distribution with mean value $2\varepsilon\Delta l\mu$ —that is, with the

probability $\exp(-2\varepsilon\Delta l\mu N)$. During the reproductive period, the female makes (at most) $l/\Delta l$ such steps. Provided that males are distributed independently at each female step, the chance of the female to remain unfertilized is independent of the shape of the pathway l traversed and equal to

$$\lim_{\Delta l \rightarrow 0} [\exp(-2\varepsilon\Delta l\mu N)]^{l/\Delta l} = \exp(-2\varepsilon l\mu N).$$

Hence, we arrive at form (17) with $\beta = 2\varepsilon l\mu$ and the area of effective search is $S = 2\varepsilon l$ under these assumptions; this form was also used in model (27).

Probability form (20) does not always satisfy (iii) as $\lim_{N \rightarrow \infty} P(N) = \mu/(1 - \mu) < 1$ for $\mu < 0.5$.

Appendix B

Extinction Boundary in Models in Table 2

Let us regard the probability of mating $P(\mu, N)$ as a function of variables μ and N . It can be rigorously shown that all probability forms (17)–(20) are increasing functions of μ for a fixed population size:

$$\frac{\partial P(\mu, N)}{\partial \mu} > 0 \quad \text{for all } N > 0 \text{ and } P(\mu, N). \quad (\text{B.1})$$

Due to $\partial P(\mu, N)/\partial N > 0$, the equation $B(N)P(1, N) - D(N) = 0$ has one non-trivial equilibrium $E^u(1)$ in the first four models in Table 2, and we assume ES scenario with two equilibria $E^u(1) < E^s(1)$ in the second four models. As all $B(N)$, $D(N)$, and $P(\mu, N)$ are sufficiently smooth, the point $E^{**} = (E^u(1), 0)$ is the limit of the boundary points $(\mu E^u(\mu), (1 - \mu)E^u(\mu))$ for $\mu \rightarrow 1$ in all models.

Inequality (B.1) implies that the equilibrium $E^u(\mu)$ (equilibrium $E^s(\mu)$) decreases (increases) with μ . As $P(0, N) = 0$ for all $N > 0$ and all probability forms (17)–(20), $\lim_{\mu \rightarrow 0} E^u(\mu) = +\infty$ in the first four models. For the same reason, the second four models possess a minimal sex ratio μ_{min} corresponding to the case of one, semistable equilibrium $E^s(\mu_{min}) = E^u(\mu_{min}) > E^u(1)$, and the boundary is then composed of a curve connecting the points E^{**} and $E^* = (\mu_{min}E^u(\mu_{min}), (1 - \mu_{min})E^u(\mu_{min}))$ and of a straight line starting in E^* . Simulations showed that the curve connecting E^{**} with E^* is concave and has positive slope in the second four models; the extinction boundary is a straight line $x = E^u(1)$ in the first four models.