

Allee effects in stochastic populations

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The Allee effect, or inverse density dependence at low population sizes, could seriously impact preservation and management of biological populations. The mounting evidence for widespread Allee effects has lately inspired theoretical studies of how Allee effects alter population dynamics. However, the recent mathematical models of Allee effects have been missing another important force prevalent at low population sizes: stochasticity. In this paper, the combination of Allee effects and stochasticity is studied using diffusion processes, a type of general stochastic population model that accommodates both demographic and environmental stochastic fluctuations. Including an Allee effect in a conventional deterministic population model typically produces an unstable equilibrium at a low population size, a critical population level below which extinction is certain. In a stochastic version of such a model, the probability of reaching a lower size a before reaching an upper size b , when considered as a function of initial population size, has an inflection point at the underlying deterministic unstable equilibrium. The inflection point represents a threshold in the probabilistic prospects for the population and is independent of the type of stochastic fluctuations in the model. In particular, models containing demographic noise alone (absent Allee effects) do not display this threshold behavior, even though demographic noise is considered an “extinction vortex”. The results in this paper provide a new understanding of the interplay of stochastic and deterministic forces in ecological populations.

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An Allee effect is a situation at low population densities in which the per-individual growth rate is an increasing function of population abundance (Allee et al. 1949, Odum and Allee 1954). The phenomenon, also termed inverse density dependence, positive density dependence, or depensation, can arise from a variety of causes, among them increased matings and breeding success, increased predation success from cooperative hunting, and increased protection from predators through aggregation. Evidence is mounting that Allee effects are not uncommon among plant and animal populations (reviewed by Dennis 1989a, Fowler and Baker 1991, Sæther et al. 1996, Groom 1998, Kuussaari et al. 1998, Wells et al. 1998, Courchamp et al. 1999a, Stephens and Sutherland 1999, Pederson et al. 2001).

While the idea that there might be a minimum density for a species to maintain itself in nature has been

around a long time (Allee 1931, 1938), density-dependent dynamics at the upper end of the abundance scale dominated population ecologists’ attentions for decades. In the 1990s, however, the growth of concern for conservation biology brought new attention to the potential importance of Allee effects in population regulation. Unfortunately, investigators in the topic have an Allee effect of their own, so to speak: old papers on the topic are hard to find, and several recent modeling studies have missed earlier related work. Models of Allee effects have a rich but sporadic history dating back to Volterra (highlights before 1990 include Volterra 1938, Kostitzin 1940, Odum and Allee 1954, Philip 1957, Mosimann 1958, Klomp et al. 1964, Bradford and Philip 1970a, b, Hsu and Frederickson 1975, Kuno 1978, Asmussen 1979, Gerritson 1980, Dennis 1981, 1989a, Dennis and Patil 1984, Jacobs 1984, Hopf and Hopf 1985, Lande 1987, Cushing 1988).

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Also, recent theoretical studies of Allee effects and population dynamics, while expanding attention in some cases to space and multiple species, have tended to be deterministic (Lewis and Kareiva 1993, Veit and Lewis 1996, Wells et al. 1998, Courchamp et al. 1999b, 2000, Scheuring 1999). Because stochastic forces loom large in influence when population numbers are small, the topic of Allee effects seems ripe for a stochastic treatment.

Dennis (1989a) constructed and analyzed deterministic, single species models of Allee effects, and examined the additional consequences of incorporating ordinary density dependence (compensation) and harvesting into the models. In addition, stochastic forces were introduced into the models. Stochastic versions of models that incorporated demographic variability alone (in the form of discrete birth-death processes) and environmental variability alone (in the form of diffusion processes) were analyzed separately. Among the results reported: if a deterministic model had a lower critical density, or unstable equilibrium, the stochastic version had an inflection point in the probability of extinction (plotted as a function of population size). Left open was the question of how Allee effects would be manifested when demographic and environmental stochastic forces are combined.

Lande (1998) pointed out that demographic stochasticity alone creates an Allee-like dynamic behavior. By transforming a diffusion process population model to a scale on which the noise is additive, Lande showed that demographic stochasticity induces a net downward component in population trajectories that is inversely proportional to population size. Below a lower critical population size, most population trajectories would have a negative short-term trend, under demographic noise alone. This demographic noise-induced lower critical size was termed a “stochastically unstable equilibrium”. Because demographic stochasticity is virtually universal in small populations, Lande concluded that the Allee-like effect induced by demographic stochasticity could help explain the observations of Allee et al. (1949) that small isolated populations often tend to become extinct.

In this paper, I argue that “real” (i.e. biological) Allee effects would produce phenomena in small, stochastic populations that are qualitatively distinct from those Allee-like phenomena produced by demographic noise alone. In particular, I show that Allee effects, but not demographic noise, lead to thresholds in the probabilities of extinction or probabilities of recovery/establishment considered as functions of population size. Demographic noise increases extinction probability, but that probability does not change appreciably between a population just above the demographic unstable equilibrium and a population just below it. By contrast, the lower critical size caused by an Allee effect marks an inflection point in the probability of extinc-

tion: the viability of a population just above critical size can be substantially enhanced over that of a population just below critical size. My earlier result on inflection points (Dennis 1989a) is generalized to include many kinds of stochastic variability: the Allee-inflection point occurs in the presence of demographic noise, environmental noise, a combination of both, or any other random forces that can be adequately approximated by diffusion processes. Also, inflection points in the probability of extinction of opposite curvature are shown to occur at locally stable equilibria. The properties of the demographic unstable point and the Allee critical point are contrasted using simple deterministic and stochastic models. The implications of the results are discussed with regard to: (1) empirically observed thresholds in the number of organisms necessary to establish viable populations in species release and translocation efforts, (2) other evidence for Allee effects, (3) discrete birth-death process models used in species preservation theory, (4) extinction vortices, (5) population viability analysis, and (6) statistical analysis of extinction data.

Deterministic Allee effect

In this section I list some deterministic population models that will serve as the underlying “skeletons” (borrowing the term from Tong 1990) of stochastic versions. A deterministic single-species model often takes the form

$$\frac{dn}{dt} = m(n), \quad (1)$$

where n is population size at time t , and $m(n)$ is a bounded, continuous function representing the dependence of the population growth rate on population size (or population density where biologically appropriate; for convenience I use the term “size” broadly throughout this paper). An equilibrium \tilde{n} is a root of

$$m(\tilde{n}) = 0. \quad (2)$$

Such an equilibrium is locally stable if the sign of $m(n)$ changes from positive to negative as n increases from just below \tilde{n} to just above \tilde{n} (nearby solution trajectories of (1) converge to \tilde{n}), locally unstable if the sign changes from negative to positive (nearby trajectories diverge from \tilde{n}). Simple textbook examples of (1) include exponential growth,

$$\frac{dn}{dt} = \lambda n - \mu n, \quad (3)$$

where λ and μ are positive constants representing the per-individual birth and death rates, and logistic growth,

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2, \quad (4)$$

where r and k are positive constants (r is the maximum per-individual growth rate and k is the “carrying capacity”, a stable equilibrium).

The per-individual growth rate in the above models is

$$g(n) = \frac{1}{n}m(n), \quad (5)$$

and roots of $g(\tilde{n}) = 0$ are also equilibria of (1). In the exponential growth model, $g(n)$ is constant for all population sizes, and in the logistic model, $g(n) = r - (r/k)n$, a linear declining function of n . The logistic can be derived as a Taylor series approximation of an unspecified decreasing function $g(n)$ near a positive stable equilibrium $\tilde{n} = k$.

An Allee effect is defined as any of a variety of biological mechanisms at low abundance levels causing $g(n)$ to be an increasing function of n (Odum and Allee 1954). If the Allee effect is severe enough at very low population sizes so that losses from the population outweigh gains, $g(n)$ will be negative and population will decrease if initiated within that range of sizes. The result is an unstable equilibrium at a low population size, a critical threshold below which a closed population is doomed to extinction.

One mechanism that can cause an Allee effect is mating limitation. Dennis (1989a) derived a Michaelis-Menton type function as a model of mating frequency or mating probability (also see McCarthy 1997), and incorporated the function as an Allee effect into the exponential and logistic growth models. The exponential growth model, modified to include mating limitation, is

$$\frac{dn}{dt} = \lambda n \frac{n}{\theta + n} - \mu n. \quad (6)$$

Here θ is a positive constant (the population size at which the per-individual birth rate is half of what it would be if coatings were not limiting). This model has an unstable equilibrium at

$$\tilde{n} = \frac{\theta\mu}{\lambda - \mu}, \quad (7)$$

which is positive provided $\lambda > \mu$. The logistic model modified to incorporate mating limitation is

$$\frac{dn}{dt} = rn - \frac{r}{k}n^2 - \frac{\lambda\theta}{\theta + n}n \quad (8)$$

(λ and θ are positive constants). Depending on parameter values, the modified logistic model can have two equilibria, an upper stable equilibrium (\tilde{n}_2) and a lower unstable equilibrium (\tilde{n}_1) given by

$$\tilde{n}_i = \frac{-B \pm \sqrt{B^2 - 4AC}}{2A}, \quad (9)$$

where $A = -r/k$, $B = r(k - \theta)/k$, and $C = \theta(r - \lambda)$. Solution trajectories initiated above \tilde{n}_1 converge to \tilde{n}_2 ; trajectories commencing below \tilde{n}_1 converge to zero (Fig. 1).

The models (6) and (8) can describe, in a phenomenological fashion, Allee effects from other biological mechanisms besides rare matings (Dennis and Patil 1984, Jacobs 1984).

Stochastic model

There are many stochastic versions of (1), and for the present analysis I adopted a general stochastic version known as a diffusion process. Diffusion processes are extremely useful and can describe a variety of biological situations. In this section, I give a brief synopsis of the advantages of the approach. A diffusion process N_t is a continuous, albeit stochastically wiggly, function of time. A diffusion process is characterized by two functions, the infinitesimal mean $m(n)$ and the infinitesimal variance $v(n)$. The infinitesimal mean specifies the underlying deterministic dynamic tendencies, while the infinitesimal variance specifies the magnitude of the stochastic fluctuations at different population sizes. Although the literature of diffusion processes is mathematically daunting, for biological modeling applications the diffusion processes are remarkably easy to use. Goel and Richter-Dyn (1974) and Nisbet and Gurney (1982) are good sources for further study.

One way to grasp the idea of a diffusion process is to envision simulating a stochastic trajectory. An approximate increment, dN_t , of the population size N_t (now in upper case to denote a random process) from time t to time $t + dt$ can be computed as

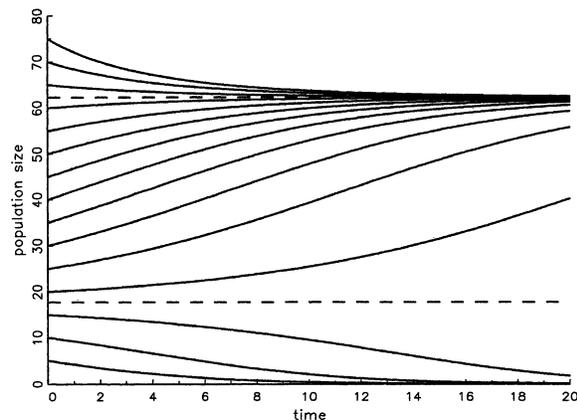


Fig. 1. Solid lines: numerical solutions of the logistic model modified to incorporate an Allee effect (eq. 8), for different initial population sizes. Parameters are $r = 0.58$, $k = 100$, $\theta = 20$, $\lambda = 0.9$. Dashed lines: local unstable and stable equilibria (eq. 9) at, respectively, $\tilde{n}_1 = 17.7$, $\tilde{n}_2 = 62.3$.

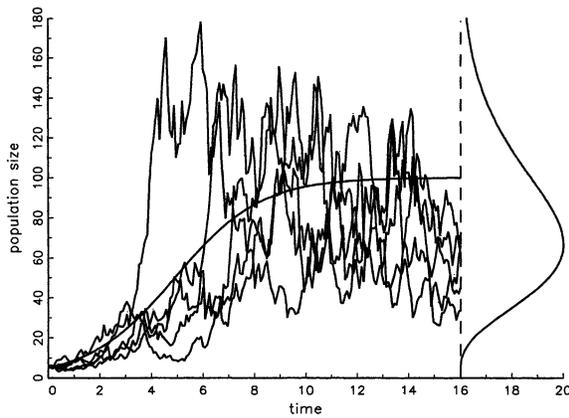


Fig. 2. Jagged lines: five realizations of a stochastic logistic model starting from an initial population size of 5. The model is a diffusion process with infinitesimal mean given by $m(n) = rn - (r/k)n^2$ and infinitesimal variance given by $v(n) = \beta n^2$ (a model of environmental variability). Smooth sigmoid line: solution of the deterministic logistic model (eq. 4). Unimodal smooth line: theoretical probability distribution of population size at time 16 (marked by dashed line). Parameters are $r = 0.6$, $k = 100$, $\beta = 0.2$.

$$dN_t = m(N_t) dt + \sqrt{v(N_t)} dW_t, \quad (10)$$

where dW_t has a normal distribution with a mean of 0 and a variance of dt . The trajectory is constructed starting at an initial population size $N_0 = n_0$, and the noise perturbations (dW_t) are generated independently each small time increment (dt). Repeated simulations of trajectories starting at n_0 give rise to a probability distribution for population size at time t (Fig. 2). With no stochastic noise ($v(n) = 0$ everywhere), the increment (10) reverts to an increment in the numerical solution of the deterministic model (1) by the Euler method. The above simulation method is serviceable for standard population models, provided the deterministic skeleton (1) is not too stiff (a numerical improvement is to calculate first the deterministic increment with an improved numerical solution method, such as Runge-Kutta, and then add the noise term). A rigorous mathematical definition of the expression (10) as a differential of the diffusion process N_t is formulated in terms of an Ito stochastic integral (see Karlin and Taylor 1981).

Diffusion processes have three major advantages as population models. The first is biological generality: many different types of stochastic models can often be approximated by diffusion processes, including density-dependent branching processes, stochastic difference equations, birth-death processes, or even stochastic projection matrices (Karlin and Taylor 1981). Results obtained for diffusion process versions of population models thus have some arguable force of generality. The second advantage is tractability: various statistical properties of diffusion processes can be derived or

approximated as pencil-and-paper formulas (Goel and Richter-Dyn 1974), although useful results for multiple-state-variable models are much scarcer. Besides being convenient for theoreticians, formulas help greatly in fitting stochastic models to data, and diffusion processes so aided have met occasionally with compelling empirical support (Costantino and Desharnais 1981, Dennis and Costantino 1988, Kemp and Dennis 1993). The third advantage is continuity: both population size and time are continuous, and so the differential equation models of population ecology translate almost directly into diffusion processes.

Depending on how stochasticity affects the population, a variety of different diffusion processes might be appropriate as the stochastic "version" of the deterministic model (1), and the literature is intricate (Turelli 1977, Capocelli and Ricciardi 1979, Tier and Hanson 1981). The main message is, if the differential equation (1) is viewed essentially as a convenient approximation to a discrete time system, and if in addition the system is subjected to unanticipative stochastic perturbations each time step, then under many circumstances the system can be approximated by a diffusion process with infinitesimal mean given by $m(n)$ and the infinitesimal variance arising from the particular type of stochastic perturbations. The effects of demographic stochastic fluctuations generally give rise to an infinitesimal variance proportional to n ($v(n) = \alpha n$, where α is a positive constant), while the effects of environmental stochastic fluctuations can be approximated with an infinitesimal variance proportional to n^2 ($v(n) = \beta n^2$, where β is a positive constant). A population for which both types of fluctuations were important can be modeled with an infinitesimal variance having summed demographic and environmental components (for instance, Tier and Hanson 1981):

$$v(n) = \alpha n + \beta n^2. \quad (11)$$

First-passage probability

In this section, I establish the result central to the ideas in this paper. Simple expressions are available for many statistical properties of diffusion processes (catalogued by Goel and Richter-Dyn 1974, Gardiner 1983). Among these properties are quantities related to the first-passage of N_t from an initial size n to a lower size a . Let $\xi(n; a, b)$ be the probability that the population reaches a before reaching an upper size b , starting at n , where $0 < a \leq n \leq b$. A standard formula gives

$$\xi(n; a, b) = \frac{\int_n^b \exp[-\phi(x)] dx}{\int_a^b \exp[-\phi(x)] dx}, \quad (12)$$

where

$$\phi(x) = 2 \int \frac{m(x)}{v(x)} dx. \quad (13)$$

In (13) the integral is an ordinary antiderivative; the (exponentiated) constant of integration cancels in numerator and denominator of (12). As a function of n , $\xi(n; a, b)$ is equal to 1 when $n = a$, is strictly monotone decreasing in the interval (a, b) , and is equal to 0 when $n = b$. The following result identifies inflection points of $\xi(n; a, b)$.

Result. If an inflection point of $\xi(n; a, b)$ occurs at a point \tilde{n} , then \tilde{n} is a point where $m(n)$ changes sign, and \tilde{n} is a solution to

$$m(\tilde{n}) = 0. \quad (14)$$

Conversely, if \tilde{n} is a solution to (14) and $m(n)$ changes sign at \tilde{n} , then an inflection point in $\xi(n, a, b)$ occurs at \tilde{n} .

Proof (informal). An inflection point is a point where a change in the sign of the second derivative of ξ occurs. The first derivative of ξ is

$$\frac{d}{dn} \xi(n; a, b) = \frac{-\exp[-\phi(n)]}{\int_a^b \exp[-\phi(x)] dx}. \quad (15)$$

Because $m(n)$ is finite, and $v(n)$ is positive and finite, $\exp[-\phi(n)]$ is positive and finite, and the first derivative (15) is negative and finite. Now, $-\ln(-d\xi/dn)$ is increasing when $d\xi/dn$ is increasing, and decreasing when $d\xi/dn$ is decreasing. Sign changes in the derivative of $-\ln(-d\xi/dn)$ correspond to sign changes in the derivative of $d\xi/dn$ (i.e. sign changes in the second derivative of ξ). The derivative of $-\ln(-d\xi/dn)$ is

$$\frac{d}{dn} \left[-\ln \left(-\frac{d\xi}{dn} \right) \right] = \phi'(n) = 2 \frac{m(n)}{v(n)}. \quad (16)$$

Sign changes in (16) correspond identically to sign changes in $m(n)$ (because $v(n)$ is positive). Because $m(n)$ is continuous, it must cross zero at a point of sign change. The inflection points of ξ are thereby obtained identically as roots of (14) at which sign changes of $m(n)$ occur.

This result shows that if \tilde{n} is a locally unstable equilibrium in the deterministic model (i.e. $m(n - \epsilon) < 0$; $m(\tilde{n} + \epsilon) > 0$, where ϵ is small), then ξ locally changes from a concave down function to a concave up function of n . Furthermore, if $m(n)$ is positive throughout the interval $a < n < b$, then ξ is concave up in that interval. Thus, ξ will have a declining J-shape (concave up) if the deterministic population growth rate is positive in the interval, and ξ will display a decreasing sigmoid (concave down to concave up) shape only if there is an

unstable equilibrium in the interval, with the equilibrium marked by the inflection point of ξ . Any kind of stochastic exponential growth model with a positive growth rate, or any type of stochastic logistic model in which the upper target size b is below carrying capacity, will have a J-shaped first-passage probability in the interval (a, b) .

Note in particular that the inflection points of ξ do not depend on the infinitesimal variance function $v(n)$. Adding or intensifying demographic noise, environmental noise, or both may increase ξ , but it will not change the qualitative shape of ξ .

For a stochastic model with an Allee effect, the inflection point in ξ represents a type of stochastic unstable equilibrium. In a model without an Allee effect, the probability of reaching a before b merely declines in a J-shaped fashion, no matter what kind of stochasticity is present. Adding more population members enhances the chances of reaching b , but there is no particular identifiable threshold. With the Allee effect, though, if the population is below the unstable equilibrium, adding more population members gives an accelerating decline in the chance of reaching a before b . This threshold in the first-passage probability is the stochastic version of a lower critical population size, below which extinction is, if not certain, disproportionately enhanced.

The amount of stochasticity, represented by the infinitesimal variance $v(n)$, affects the abruptness of the change in the extinction curve at \tilde{n} . The degree of curvature change at \tilde{n} depends on the steepness of the second derivative term (16). If stochastic forces are small in comparison to deterministic forces, the ratio $m(n)/v(n)$ in (16) crosses zero steeply at \tilde{n} , and the first-passage probability (15) changes curvature abruptly. In the limit of no stochasticity, of course, the first-passage probability (15) is a step function ($\xi(n; a, b) = 1$, $n < \tilde{n}$; $\xi(n; a, b) = 0$, $n > \tilde{n}$). If, however, stochastic forces are large in comparison to deterministic forces, the curvature change at \tilde{n} will not be very evident; ξ will look almost like a decreasing straight line.

Demographic stochasticity

A stochastic version of the simple exponential growth model (3) illustrates the effects of demographic stochasticity alone. A diffusion process with

$$m(n) = \lambda n - \mu n, \quad (17)$$

$$v(n) = \alpha n, \quad (18)$$

is a general model of exponential growth with demographic-type noise fluctuations. From (12) and (13), one finds that

$$\phi(n) = 2 \int \frac{(\lambda - \mu)n}{\alpha n} dn = \frac{2(\lambda - \mu)}{\alpha} n \quad (19)$$

and

$$\xi(n; a, b) = \frac{e^{-\frac{2(\lambda - \mu)}{\alpha} n} - e^{-\frac{2(\lambda - \mu)}{\alpha} b}}{e^{-\frac{2(\lambda - \mu)}{\alpha} a} - e^{-\frac{2(\lambda - \mu)}{\alpha} b}} \quad (20)$$

The function ξ has a decreasing exponential shape, starting at $\xi = 1$ when $n = a$, and ending at $\xi = 0$ when $n = b$ (Fig. 3). Increasing the value of α always increases the probability of hitting a before b , but it does not change the qualitative shape of the function.

The probability of extinction is approximately the probability of attaining a very small size a before attaining a very large size b . The probability of extinction starting from population size n under this model is found from (20) by letting $a \rightarrow 0$ and $b \rightarrow \infty$. Thus,

$$\xi(n; 0, \infty) = e^{-\frac{2(\lambda - \mu)}{\alpha} n} \quad (21)$$

Interestingly, (21) is the tail probability of an exponential probability distribution. If a random variable X has an exponential distribution on the positive real line with a mean of $\alpha/[2(\lambda - \mu)]$, then $\xi(n; 0, \infty) = P[X > n]$. (Also, (20) is the tail probability of an exponentially distributed random variable confined between a and b .)

Lande (1998) noted the following Allee-like phenomenon that is induced by demographic noise alone. He used the fact from diffusion process theory that a diffusion process can be transformed to a scale with a

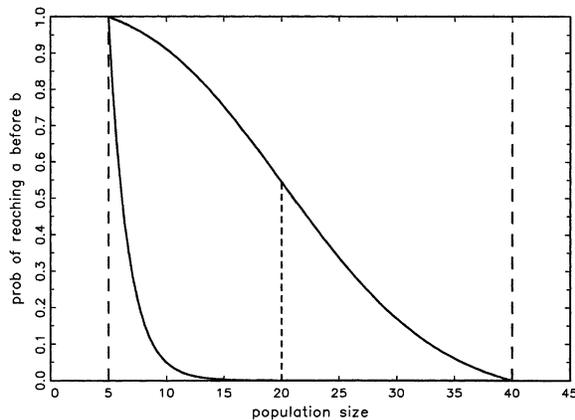


Fig. 3. Solid lines: $\xi(n; a, b)$, the probability of reaching population size a before size b , graphed as a function of initial population size n , for (lower line) exponential growth with demographic noise (eq. 20), and (upper line) exponential growth with Allee effect and demographic noise (eq. 34). Dashed lines: population sizes $a = 5$ and $b = 40$. Short-dashed line: Allee critical point (unstable equilibrium) at $\bar{n} = 20$ indicates location of inflection point in $\xi(n; a, b)$. Parameters are $\lambda = 0.9$, $\mu = 0.3$, $\theta = 40$, $\alpha = 2$.

constant infinitesimal variance. If a new diffusion process, $Y_t = h(N_t)$, is defined as a transformation of the original diffusion process, where the function h is given by

$$h(n) = \int \frac{dn}{\sqrt{v(n)}} \quad (22)$$

then the diffusion process Y_t has an infinitesimal mean of

$$m_Y(y) = \frac{m(n) - \frac{1}{4}v'(n)}{\sqrt{v(n)}} \quad (23)$$

(with $n = h^{-1}(y)$) and an infinitesimal variance of

$$v_Y(y) = 1 \quad (24)$$

(Goel and Richter-Dyn 1974). On the new scale, the noise is merely additive and the solution trajectory of the deterministic model given by $dy/dt = m_Y(y)$ traces the *most probable transition path* (Dekker 1978). For a small time interval dt , the transition probability distribution for Y_t is approximately normal with a mean (and median and mode) of $y_0 + m_Y(y_0) dt$ (Risken 1984). Lande noted from (23) that there can be a population size, \bar{n} , at which the infinitesimal mean (23) is zero. That population size is a root of

$$m(\bar{n}) - \frac{1}{4}v'(\bar{n}) = 0. \quad (25)$$

If the model has demographic noise alone, then \bar{n} is a root of

$$m(\bar{n}) - (\alpha/4) = 0. \quad (26)$$

For the exponential growth model with demographic noise, one finds using (17) and (26) that \bar{n} is located at

$$\bar{n} = \frac{\alpha}{4(\lambda - \mu)}. \quad (27)$$

Note that (26) is the expression for the equilibrium of a deterministic population (1) subjected to constant rate harvesting, a situation known for causing lower unstable equilibria (Brauer and Sanchez 1975). On the transformed Y -scale, the value $\bar{y} = h(\bar{n})$ represents an unstable equilibrium in the equation for the most likely sample path. If the initial population size is greater than \bar{n} , then the most likely sample path is increasing. If, however, the initial size is less than \bar{n} , the most likely sample path decreases. In this sense, stochastic trajectories diverge probabilistically from \bar{n} . Demographic stochasticity apparently gives rise to a different sort of lower critical population size, with properties different from those caused by an Allee effect.

The first-passage result (14), however, demonstrates that the transition in dynamic behavior near \bar{n} is “smooth” on the original untransformed scale, that is, no sudden change in first-passage outcomes would be discernible between trajectories starting from $\bar{n} - \epsilon$ and those starting from $\bar{n} + \epsilon$. The decrease in the probability of reaching *any* lower size a before *any* upper size b (where $a < \bar{n} < b$) would not be any more noteworthy near \bar{n} than anywhere else.

On the transformed scale, of course, the first-passage result (14) applies to the diffusion process Y_t just as it does to N_t . The probability that Y_t reaches a lower size y_a before an upper size y_b , starting from initial size y would have an inflection point at the demographic unstable point $\bar{y} = h(\bar{n})$. The original abundance scale, however, has been stretched and/or compressed nonlinearly by the transformation $Y_t = h(N_t)$, and that inflection point does not show up at population size \bar{n} on the original scale.

One should note that *other* transformations besides the constant-variance transformation (22) could produce infinitesimal means with different equilibria on the transformed scale. Those equilibria would not show up either as inflection points in the first-passage probability on the original scale. There is no particular reason to regard the constant-variance transformation as the “true” scale for describing first-passage properties.

Allee effect plus demographic stochasticity

An Allee effect, in contrast to the effect of demographic stochasticity alone, produces a threshold-like dynamic behavior near a deterministic unstable equilibrium, \bar{n} , regardless of the type of noise present. The threshold-like behavior is manifested stochastically as an inflection point at population size \bar{n} in the probability of attaining size a before size b .

For instance, the demographic-stochastic exponential growth model, with infinitesimal moments given by (17) and (18), can be modified to accommodate an Allee effect. The deterministic model (6), with the mating limitation function, provides the infinitesimal mean, with the infinitesimal variance remaining in its demographic form:

$$m(n) = \lambda n \frac{n}{\theta + n} - \mu n, \quad (28)$$

$$v(n) = \alpha n. \quad (29)$$

The first-passage probability for this model turns out to be related to the gamma probability distribution. From (13), one finds that

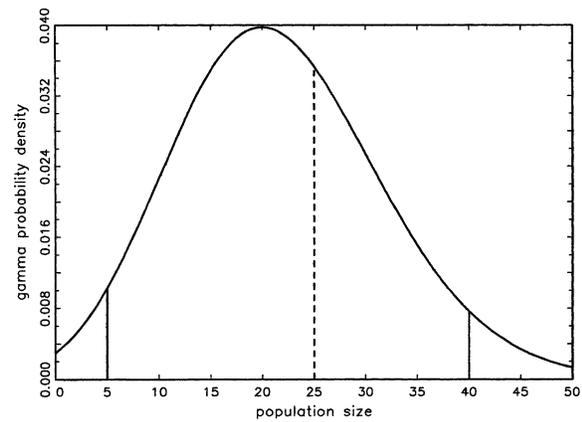


Fig. 4. The probability of reaching population size a before size b from size n (eq. 34), under exponential growth with Allee effect and demographic noise, is the area under a shifted gamma probability density curve between n (dashed line) and b (right vertical solid line) divided by the area under the gamma curve between a (left vertical solid line) and b .

$$\begin{aligned} \phi(x) &= 2 \int \frac{\lambda x^2}{\alpha x(\theta + x)} dx - 2 \int \frac{\mu x}{\alpha x} dx \\ &= \frac{2\lambda}{\alpha} [x - \theta \ln(\theta + x)] - \frac{2\mu}{\alpha} x \\ &= \frac{2(\lambda - \mu)}{\alpha} x - \frac{2\lambda\theta}{\alpha} \ln(\theta + x). \end{aligned} \quad (30)$$

The integrands in the formula (12) for ξ are all in the form

$$e^{-\phi(x)} = (\theta + x)^{\frac{2\lambda\theta}{\alpha}} e^{-\frac{2(\lambda - \mu)}{\alpha} x}. \quad (31)$$

This function is like the probability density function of a gamma distribution (Evans et al. 1993), without the normalization constant, that has been shifted left to start at $x = -\theta$ instead of $x = 0$ (Fig. 4). The integrals in (12) can be expressed in terms of areas under a gamma probability density function, after multiplying numerator and denominator by the normalization constant. Define

$$F(z; p, q) = \int_0^z \frac{q^p}{\Gamma(p)} x^{p-1} e^{-qx} dx \quad (32)$$

as the cumulative distribution function of a gamma distribution ($p > 0$, $q > 0$, and the normalization constant $q^p/\Gamma(p)$ scales the function to integrate to unity on $(0, \infty)$). The integral in the numerator of (12), using (31) and (32), becomes

$$\begin{aligned} &\int_n^b (\theta + x)^{\frac{2\lambda\theta}{\alpha}} e^{-\frac{2(\lambda - \mu)}{\alpha} x} dx \\ &= \frac{\Gamma(p)}{q^p} e^{\frac{2(\lambda - \mu)\theta}{\alpha}} [F(b + \theta; p, q) - F(n + \theta; p, q)], \end{aligned} \quad (33)$$

where $p = (2\lambda\theta/\alpha) + 1$ and $q = 2(\lambda - \mu)/\alpha$. The function $\xi(n; a, b)$, after cancellation of the constants in numerator and denominator of (12), becomes

$$\xi(n; a, b) = \frac{F(b + \theta; p, q) - F(n + \theta; p, q)}{F(b + \theta; p, q) - F(a + \theta; p, q)} \quad (34)$$

The probability ξ is seen to be the area from n to b under a left-shifted gamma density function, divided by the area from a to b (Fig. 4).

The probability of extinction is found by letting $a \rightarrow 0$ and $b \rightarrow \infty$ in (34):

$$\xi(n; 0, \infty) = \frac{1 - F(n + \theta; p, q)}{1 - F(\theta; p, q)} \quad (35)$$

This expression is the right-tail probability, from n onward, of the shifted gamma, divided by the right-tail probability from 0 onward. As θ approaches zero, the first-passage probability (21) for the ordinary stochastic exponential growth model is recovered as the tail of an exponential distribution.

The mode of a gamma probability density function (the integrand in (32)) is $(p - 1)/q$. Thus, the left-shifted gamma integrand (31) has a mode at

$$\frac{(p - 1)}{q} - \theta = \frac{\theta\mu}{\lambda - \mu} = \tilde{n}, \quad (36)$$

which is the unstable equilibrium (7) in the deterministic model. The mode of the integrand (Fig. 4) produces the inflection point in ξ (Fig. 3). When n is below \tilde{n} , the tail probability in the numerator of (34) or (35) decreases in a concave downward fashion (Fig. 3). Above \tilde{n} , the tail probability decreases in a convex upward fashion similar to the tail probability of an exponential distribution. The inflection point in ξ is at \tilde{n} , the lower critical population size.

Where is the demographic unstable point? From (26), \tilde{n} is identical to an unstable equilibrium in a harvesting model, and so in general \tilde{n} will be greater than an unstable equilibrium \bar{n} in a model without harvesting. After substituting (28) into (26), it is straightforward to solve the quadratic for the demographic unstable point \bar{n} . Writing $\bar{n}_d = (\alpha/4)/(\lambda - \mu)$ for the demographic unstable point (27) in the model without an Allee effect, one finds for the Allee effect model that

$$\bar{n} = \frac{1}{2}(\tilde{n} + \bar{n}_d) + \frac{1}{2}\sqrt{(\tilde{n} + \bar{n}_d)^2 + \theta\alpha/4}. \quad (37)$$

If demographic stochasticity is small, α and \bar{n}_d are small, and the demographic unstable point \bar{n} is near (slightly above) the Allee critical size \tilde{n} .

Upper stable equilibrium

Inflection points in first-passage probabilities are a general phenomenon and represent the remnant ghosts of deterministic forces after stochasticity is added. Any ecological factor besides an Allee effect that produces an unstable equilibrium, such as constant rate harvesting, will lead to a similar inflection point in the first-passage probability. Moreover, the result (14) on inflection points applies to stable as well as unstable equilibria. In this section, the analysis of Allee effects is extended to incorporate an upper stable equilibrium population size.

When result (14) is applied to the case of a stable equilibrium, the inflection point in $\xi(n; a, b)$ marks a change from concave up to concave down as n increases, a shape change opposite to that of an unstable equilibrium. As an example, consider a demographic stochastic version of the logistic model (8). A version with environmental stochasticity was studied by Leigh (1968), Dennis and Patil (1984), Dennis and Costantino (1988), and Dennis (1989b); a version with both demographic and environmental stochasticity was studied by Tier and Hanson (1981). The infinitesimal moments of the version with demographic noise alone are:

$$m(n) = rn - (r/k)n^2, \quad (38)$$

$$v(n) = \alpha n. \quad (39)$$

From (13), one finds that

$$-\phi(x) = -\frac{2r}{\alpha}x + \frac{r}{\alpha k}x^2, \quad (40)$$

a quadratic function of x . The first-passage probability (12) becomes

$$\xi(n; a, b) = \frac{\int_n^b e^{-\frac{2r}{\alpha}x + \frac{r}{\alpha k}x^2} dx}{\int_a^b e^{-\frac{2r}{\alpha}x + \frac{r}{\alpha k}x^2} dx} \quad (41)$$

The quadratic function (40) in the exponent of the numerator integrand has a minimum at $\tilde{n} = k$, and so the inflection point of (41) occurs at the carrying capacity (stable equilibrium), k (provided $a < k < b$). For the entire range of abundances below k , the shape of $\xi(n; a, b)$ is concave up (Fig. 5).

The version of the above model that incorporates an Allee effect has infinitesimal mean based on the deterministic growth rate (8) and infinitesimal variance in the demographic form:

$$m(n) = rn - \left(\frac{r}{k}\right)n^2 - \frac{\lambda\theta n}{\theta + n}, \quad (42)$$

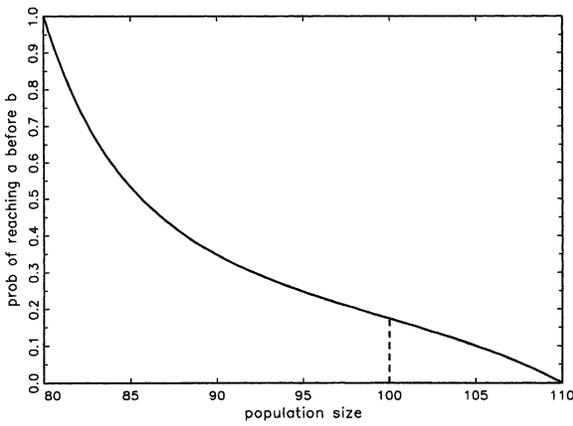


Fig. 5. Solid line: $\xi(n; a, b)$, the probability of reaching a before b from initial size n , graphed as a function of n , for logistic growth with demographic noise (eq. 41). Dashed line: stable equilibrium at $\tilde{n} = 100$ indicates location of inflection point in $\xi(n; a, b)$. Parameters are $r = 0.6$, $k = 100$, $\alpha = 1$, $a = 80$, $b = 110$.

$$v(n) = \alpha n. \quad (43)$$

The formula (13) for $\phi(x)$ yields:

$$\phi(x) = \frac{2r}{\alpha} x - \frac{r}{k\alpha} x^2 - \frac{2\lambda\theta}{\alpha} \ln(\theta + x). \quad (44)$$

The formula (12) for $\xi(n; a, b)$ in turn produces

$$\xi(n; a, b) = \frac{\int_a^n (\theta + x)^{\frac{2\lambda\theta}{\alpha}} e^{-\frac{2r}{\alpha}x - \frac{r}{k\alpha}x^2} dx}{\int_b^a (\theta + x)^{\frac{2\lambda\theta}{\alpha}} e^{-\frac{2r}{\alpha}x - \frac{r}{k\alpha}x^2} dx}. \quad (45)$$

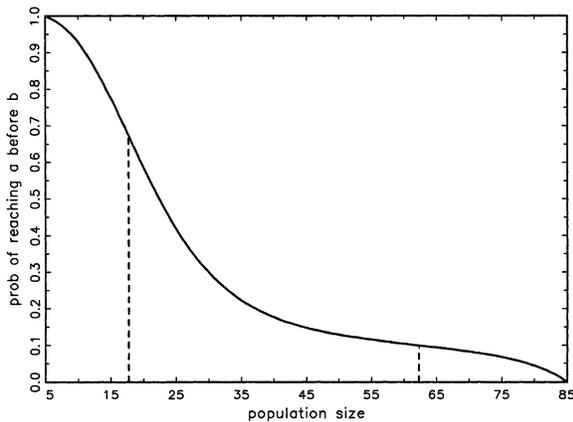


Fig. 6. Solid line: $\xi(n; a, b)$, the probability of reaching a before b from initial size n , graphed as a function of n , for logistic growth with Allee effect and demographic noise (eq. 45). Dashed lines: local unstable and stable equilibria (eq. 9) at, respectively, $\tilde{n}_1 = 17.7$, $\tilde{n}_2 = 62.3$ indicate locations of inflection points in $\xi(n; a, b)$. Parameters are $r = 0.58$, $k = 100$, $\theta = 20$, $\lambda = 0.9$, $\alpha = 1$, $a = 5$, $b = 85$.

The integrals in (45) are not expressible in terms of familiar probability distributions. The local maximum and minimum of the integrand correspond with the unstable and stable equilibria (9) of the deterministic model (8). The function $\xi(n; a, b)$ has an Allee-type inflection point at the lower unstable equilibrium, in addition to the inflection point at the upper stable equilibrium (Fig. 6).

Discussion

Empirical evidence of thresholds

Various studies of species translocations, introductions, and extinctions have provided evidence that threshold abundances are frequently necessary for a species' establishment and continued survival (Beirne 1975, Griffith et al. 1989, Berger 1990, Hopper and Roush 1993, Green 1997). The analysis presented here shows that such evidence of thresholds is not qualitatively consistent with demographic stochasticity alone, but rather is suggestive of a lower unstable equilibrium in density-dependent forces. Demographic stochasticity enhances the chance of extinction, but the effect of reducing population members on that chance remains smooth and incremental throughout the range of possible abundances.

Other evidence for Allee effects

In the decade since the reviews by Dennis (1989a) and Fowler and Baker (1991), additional evidence, sometimes experimental (Widén 1993, Groom 1998, Pederson et al. 2001), sometimes observational (Lamont and Klinkhamer 1993, Lamont et al. 1993, Levitan and Petersen 1995, Ghazoul et al. 1998, Kuussaari et al. 1998), sometimes theoretical (Dobson and Lyles 1989, Beier 1993, Swart et al. 1993, Fauvergue et al. 1995, Pfister and Bradbury 1996, Veit and Lewis 1996, Grevstad 1999, Shelton and Healey 1999, Frank and Brickman 2000), sometimes anecdotal (Makaloff 1997, Gerber et al. 2000) of the importance of Allee effects in natural populations has been reported (see also the more recent reviews by Sæther et al. 1996, Kuussaari et al. 1998, Wells et al. 1998, Courchamp et al. 1999a, Stephens and Sutherland 1999). Pettersson (1985), in a paper missed by reviewers, showed how the ordinary demographic birth-death model grossly underestimated extinction risk in a woodpecker population because the birds suffered reduced breeding success at low numbers. Studies in some systems turned up no evidence for Allee effects (Myers et al. 1995, Sæther et al. 1996, Kindvall et al. 1998). The present analysis places the dynamics expected in populations, with or without Allee effects, in a more realistic stochastic context and reemphasizes

the potentially critical influence of Allee effects in small populations.

Discrete birth-death processes

A different type of stochastic model known as discrete birth-death processes is used frequently in species preservation theory (MacArthur and Wilson 1967, Richter-Dyn and Goel 1972, Dennis 1981, 1989a, Wright and Hubbell 1983, Goodman 1987, Wissel and Stöcker 1991, Allen et al. 1992, Wissel and Zaslack 1994). Discrete birth-death processes take population size to be integer-valued; Bailey (1964), Nisbet and Gurney (1982), and Renshaw (1991) provide exceptionally readable treatments. Birth-death processes can be approximated by diffusion processes (Nisbet and Gurney 1982) and vice versa (Wissel 1989).

The extinction probabilities (35) and (21) for the diffusion process models with and without Allee effects are qualitatively similar to results obtained for discrete birth-death processes (Dennis 1981, 1989a). For a birth-death process version of the simple exponential growth model (3), the extinction probability was the summed right-tail probabilities of a geometric distribution, a J-shaped discrete probability distribution resembling the exponential distribution in (21). For the birth-death process version of the model with an Allee effect (6), the extinction probability was the summed right-tail probabilities of a negative binomial distribution, a mound-shaped distribution resembling the gamma in (35). The mound shape of the negative binomial produced an inflection point in the extinction probability, located at the (integerized) deterministic unstable equilibrium (Dennis 1981, 1989a).

It should be noted that birth-death process models with linear birth and death rates, such as the exponential growth model built from (3), are based implicitly on demographic stochasticity (Goodman 1987, Wissel and Schmitt 1987). The birth-death process version of exponential growth therefore has a demographic unstable point, but any consequences for population size as a result of the demographic unstable point remain obscure at present. By contrast, the underlying deterministic unstable equilibrium in the Allee effects model is manifested clearly in the probabilistic behavior of the discrete birth-death process version.

Extinction vortex

Gilpin and Soulé (1986) discussed four biological phenomena in small populations that they called the "extinction vortices". The phenomena were ways in which the chance of extinction is exacerbated by small population sizes, creating a vicious cycle from which recovery is difficult. The four extinction vortices were demo-

graphic variability, fragmentation, loss of fitness from reduced genetic heterozygosity, and loss of evolutionary responsiveness from reduced heterozygosity. Evidence of real vortex effects on population dynamics and extinction risk has emerged through careful demographic and genetics studies (Soulé and Mills 1998, Westemeier et al. 1998; Fischer et al. 2000). The qualitative patterns of extinction risk produced by demographic variability alone have been described here; the other three vortices might conceivably produce extinction patterns resembling those of Allee effects. In view of the accumulating empirical evidence and the alarming theoretical consequences, I propose that de facto Allee effects be acknowledged as the fifth extinction vortex.

PVA and extinction risk

Conservation biologists tend to prefer stochastic simulation models with more biological detail when conducting a population viability analysis for a particular species or population (Boyce 1992). Such models are complex, with many state variables to represent different sub-populations, life stages, or even individual population members. While simple models can often capture essential properties of complex ones, biological managers faced with critical policy decisions are understandably more comfortable with analyses that incorporate biological variables.

One biological detail that is frequently overlooked in PVA is the prospect of an Allee effect. Not only could an Allee effect substantially alter the chances of extinction, but in addition, the exclusion of the prospect from the analysis could result in a misleading underestimate of the actual risks to the population. Unfortunately, the estimation of the presence and degree of an Allee effect in a single population is fraught with difficulties. Because of this, Dennis et al. (1991) suggested that PVA should focus where possible not on extinction but rather on the attainment of some low (but positive) population size of policy interest, set high enough to avoid the possibility of small population phenomena such as Allee effects.

Testing for an Allee effect in data

Formulating the problem of Allee effects in a stochastic framework is a potential key to testing for an Allee effect in species colonization or translocation data. In some systems, it is possible to record the fates of numerous similar populations that started out at different population sizes (Crowell 1973, Mason 1977, Toft and Schoener 1983, Griffith et al. 1989, Berger 1990, Hopper and Roush 1993, Pimm et al. 1993, Green 1997, Berggren 2001). The analysis in the present paper,

showing that the first-passage probability is the right-tail area of a probability distribution, gives some justification to the use of a cumulative distribution function (such as in logistic regression or probit analysis) to model a population's chance of survival as a function of initial size. In such an analysis, one could alternatively use the cumulative distribution function of a flexible parametric distribution (like the gamma or Weibull) containing both sigmoid and exponential-like shapes, to test between the presence and absence of an inflection point as competing statistical hypotheses.

Concluding remarks

Stephens et al. (1999) argued for retaining some terminology distinction between biological Allee effects (mechanisms leading to actual reductions in mean fitness at low abundances) and those population-level effects identified by Lande (1998) that are caused solely by increases in variability at low abundances. The distinction can be summarized as mechanisms which affect $m(n)$ and mechanisms which affect only $v(n)$. Because only mechanisms which create unstable equilibria in $m(n)$ will appear as thresholds in first-passage probabilities, the distinction between biological Allee effects (Allee 1938) and noise-induced phenomena (Horsthemke and Lefever 1984) is critical to understanding patterns of extinction in natural populations.

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