



Weak Allee effects population growth models in a random environment

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Abstract

Based on a deterministic model of population growth with weak Allee effects, we propose a general stochastic model that incorporates environmental random fluctuations in the growth process. We study the model properties, existence and uniqueness of solution, the stationary behavior and mean and variance of the time to extinction of the population. We then consider as an example the particular case of a stochastic model with Allee effects based on the classic logistic model.

Keywords: Allee effects; population growth; random environments; extinction times.

1. Introduction

Populations live in environments with limited resources (density-dependence) and so one expects that, as the population size gets larger, the resources available for individual growth and reproduction become scarcer, resulting in smaller *per capita* growth rates. So, if $X(t)$ is the population size at time t , we expect that the *per capita* growth rate $\frac{1}{X} \frac{dX}{dt}$ (from here on abbreviated called growth rate) will be a decreasing function of population size. For many populations, however, this rule fails for low population sizes due to several causes, such as the difficulty of its individuals in finding mating partners (particularly if the population is geographically dispersed) or the inability to set up an appropriate group defense against predators.

These are the so-called Allee effects, which were first described in Allee *et al.* (1949). There are two kinds of Allee effects, weak Allee effects and strong Allee effects. When a population has a "critical size or density" below which the growth rate is negative (which implies that the population will decrease) and above which it becomes positive, we speak of a strong Allee effect. On the other hand, when a population does not exhibit a "critical size or density" but at low densities the growth rate increases with increasing density, we speak of a weak Allee effect.

When the environment is subjected to random fluctuations, one can add to the deterministic (ordinary differential equation) model an extra term to account for the effect of environmental fluctuations in the growth rate, thus obtaining stochastic differential equation (SDE) models. This allows us to study the consequences of environmental variability and the extinction behavior, as well as the extinction time of the population.

The study of general SDE population growth models without Allee effects can be seen in Braumann (2007, 2008). General and specific SDE models with strong Allee effects were studied in Braumann and Carlos (2013); in this paper, we also study the first passage time through an extinction threshold (extinction time), based on previous results on extinction time for certain class of SDE models (see Braumann et al 2009, 2011, Carlos, Braumann and Filipe 2013, Filipe, Braumann and Carlos 2014).

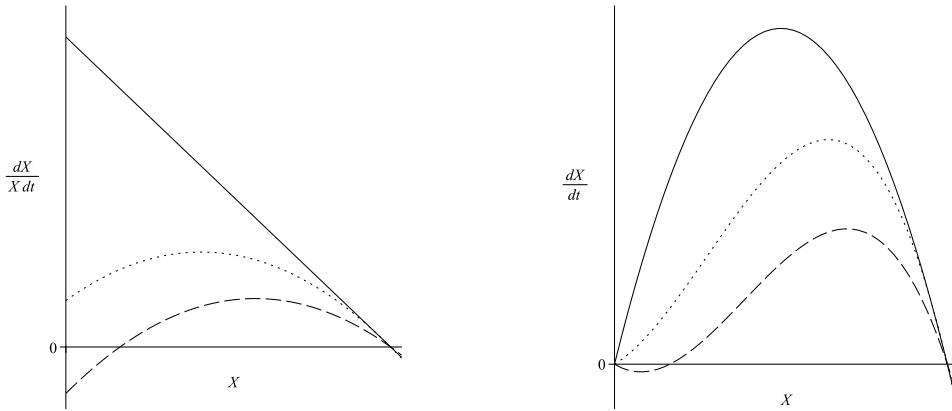


Figure 1: Example (logistic or logistic-like models) of the (*per capita*) growth rate $\frac{1}{X} \frac{dX}{dt}$ (on the left) and the total population growth rate dX/dt (on the right) as a function of population size. The solid line represents a model which no Allee effects, the dashed line represents a model with strong Allee effects and the dotted line represents a model with weak Allee effects.

Here, based on deterministic models with weak Allee effects, we propose and perform similar studies for general SDE models for population growth in random environments with weak Allee effects. A particular specific model, inspired by the classical logistic model, is also presented for illustration purposes.

2. Model

Let $X = X(t)$ be the population size at time $t > 0$ and $L > 0$ a positive constant. We propose as a general model with weak Allee effects that the (*per capita*) growth rate be the form

$$\frac{1}{X} \frac{dX}{dt} = f(X), \quad (1)$$

where $f(X)$ is a real C^1 function defined for $X > 0$ such that f increases for $X < L$, decreases for $X > L$ and $0 < f(0^+) < +\infty$. Suppose $f(X) > 0$ for $X < K$ and $f(X) < 0$ for $X > K$, with $K > 0$ carrying capacity of the environmental. We assume that the initial size $X(0) = x$ is known.

In a randomly fluctuating environment, the growth rate varies randomly and expression (1) should now be interpreted as describing its average behavior and, since growth is a multiplicative type process, the geometric average is the appropriate one to consider. We then need to add the effect of environmental fluctuations on the growth rate, which we assume to be of the white noise type, of the form $\sigma\epsilon(t)$, where $\epsilon(t)$ is a standard continuous-time white noise and $\sigma > 0$ is the noise intensity, assumed to be constant and independent of population size. Therefore, assuming expression (1) represents the geometric average growth rate, it can be seen in Braumann (2007) that the appropriate stochastic calculus to use is the Stratonovich calculus, and so we shall use it here. We obtain the stochastic differential equation (SDE)

$$\frac{1}{X} \frac{dX}{dt} = f(X) + \sigma\epsilon(t), \quad (2)$$

with $X(0) = x$ known.

The solution $X(t)$ exists and is unique up to an explosion time (see, for instance, Arnold (1974)). We can show that there is no explosion and therefore, the solution exists and is unique for all $t \geq 0$. The solution $X(t)$ is a homogeneous diffusion process with drift coefficient

$$a(x) = x \left(f(x) + \frac{\sigma^2}{2} \right) \quad (3)$$

and diffusion coefficient

$$b^2(x) = \sigma^2 x^2. \quad (4)$$

Let us define, in the interior of the state space, the scale and speed measures of $X(t)$. The scale density is

$$s(y) := \exp\left(-\int_n^y \frac{2a(\theta)}{b^2(\theta)} d\theta\right) = \frac{n}{y} \exp\left(-\frac{2}{\sigma^2} \int_n^y \frac{f(\theta)}{\theta} d\theta\right) \quad (5)$$

and the speed density is

$$m(y) := \frac{1}{b^2(y)s(y)} = \frac{1}{n\sigma^2 y} \exp\left(\frac{2}{\sigma^2} \int_n^y \frac{f(\theta)}{\theta} d\theta\right), \quad (6)$$

where n is an arbitrary (but fixed) point in the interior of the state space. The corresponding "distribution" functions are $S(z) = \int_c^z s(y)dy$ and $M(z) = \int_c^z m(y)dy$, the scale function and speed function, respectively, where c is an arbitrary (but fixed) point in the interior of the state space. The scale measure is define for intervals (a, b) by $S(a, b) = S(b) - S(a)$ and the speed measure is defined by $M(a, b) = M(b) - M(a)$.

The state space has boundaries $X = 0$ and $X = +\infty$.

One can see that $X = 0$ is non-attracting and therefore, "mathematical" extinction has zero probability of occurring. It suffices to show that, for some $x_0 > 0$, $S(0, x_0) = \int_0^{x_0} s(y)dy = +\infty$ (see, for instance, page 228 of Karlin and Taylor 1981). This is indeed the case, since, for $0 < x_0 < n$ and $0 < y \leq x_0 < L$, we have $S(0, x_0] \geq \int_0^{x_0} \frac{n}{y} dy = +\infty$.

One can see that $X = +\infty$ is non-attracting and, therefore, explosions can not occur and the solution exists and is unique for all $t > 0$. It suffices to show that, for some $x_0 > 0$, $S[x_0, +\infty) = \int_{x_0}^{+\infty} s(y)dy = +\infty$. This is indeed the case, since, for $0 < n < x_0$ and $K < x_0 \leq y < +\infty$, we have

$$S[x_0, +\infty) \geq \exp\left(-\frac{2}{\sigma^2} \int_n^{x_0} \frac{f(\theta)}{\theta} d\theta\right) \int_{x_0}^{+\infty} \frac{n}{y} dy = +\infty.$$

Contrary to the deterministic model (1), the stochastic model (2) does not have an equilibrium point, but there may exist an equilibrium probability distribution for the population size, called the stationary distribution, with a probability density function $p(y)$, known as stationary density. Indeed, since the boundaries are non-attracting, the stationary density exists if $M = \int_0^{+\infty} m(y)dy < +\infty$ (see page 241 of Karlin and Taylor 1981) and is given by $p(y) = \frac{m(y)}{M}$, with $0 < y < +\infty$.

We will now prove that, in model (2), the population size has a stationary density. We need to show that $M < +\infty$. Let $y_1 < K < y_2$ be such that $0 < y_1 < n < y_2 < +\infty$ and $n < L$. So $0 < y_1 < n < L < K < y_2$. Break the integration interval,

$$M = M_1 + M_2 + M_3 = \int_{0^+}^{y_1} m(y)dy + \int_{y_1}^{y_2} m(y)dy + \int_{y_2}^{+\infty} m(y)dy.$$

We first show that M_1 is finite. Let $y \in (0, y_1]$ and $\theta \in [y, n]$. As $0 < f(0^+) < +\infty$, we have

$$m(y) \leq \frac{1}{n^2 \sigma^2} \left(\frac{y}{n}\right)^{\frac{2}{\sigma^2} f(0^+) - 1},$$

because f is increasing. Therefore $M_1 < +\infty$.

We now prove that $M_3 < +\infty$. Let $y \in [y_2, +\infty)$ and $\theta \in [n, y]$. Decompose

$$\frac{2}{\sigma^2} \int_n^y \frac{f(\theta)}{\theta} d\theta = \frac{2}{\sigma^2} \int_n^{y_2} \frac{f(\theta)}{\theta} d\theta + \frac{2}{\sigma^2} \int_{y_2}^y \frac{f(\theta)}{\theta} d\theta = A + B(y).$$

Then

$$m(y) \leq \frac{1}{n\sigma^2 y} \exp(A) \exp\left(\frac{2}{\sigma^2} f(y_2) \ln \frac{y}{y_2}\right).$$

Therefore, we get

$$M_3 = c_1 \int_{y_2}^{+\infty} y^{\frac{2}{\sigma^2} f(y_2) - 1} dy < +\infty,$$

with c_1 constant.

Finally, it is easy to see that $M_2 < +\infty$ because it is the integral of a continuous function in a closed interval. The stationary density is given by

$$p(y) = D \frac{1}{\sigma^2 y} \exp\left(\frac{2}{\sigma^2 y} \exp\left(\frac{2}{\sigma^2} \int_n^y \frac{f(\theta)}{\theta} d\theta\right)\right), \quad (7)$$

where $D = \left(\int_0^{+\infty} \frac{1}{\sigma^2 y} \exp\left(\frac{2}{\sigma^2 y} \exp\left(\frac{2}{\sigma^2} \int_n^y \frac{f(\theta)}{\theta} d\theta\right)\right) dy\right)^{-1}$ is a constant such that $\int_0^{+\infty} p_y(y) dy = 1$.

As shown, "mathematical" extinction has zero probability of occurring, but we prefer to use the concept of "realistic" extinction, meaning the population dropping below an extinction threshold $q > 0$ (for example, $q = 1$). We are interested in the extinction time, i.e. the time

$$T_q = \inf\{t > 0 : X(t) = q\}$$

required for the population to reach the extinction threshold for the first time. Assuming $0 < q < x < +\infty$, we can write (see, for instance, Braumann *et al.* (2009)) expressions for the n -th order moment of T_q :

$$M_q^{(n)}(x) = E[(T_q)^n | X(0) = x] = 2 \int_q^x s(\zeta) \int_\zeta^{+\infty} n M_q^{(n-1)}(\theta) m(\theta) d\theta d\zeta. \quad (8)$$

Since $M_q^{(0)}(x) = 1$, one can iteratively obtain the moments of any arbitrary order of T_q . The expression obtained above is valid for sufficiently regular homogeneous diffusion processes with drift coefficient a and diffusion coefficient b^2 by solving known differential equations (see, for instance, Karlin and Taylor (1981)) for $E[(T_{qQ})^n | X(0) = x]$, letting $Q \rightarrow +\infty$ and performing some algebraic manipulations. In particular, the expression for the mean of the first passage time is

$$E[T_q | X(0) = x] = 2 \int_q^x s(\zeta) \int_\zeta^{+\infty} m(\theta) d\theta d\zeta. \quad (9)$$

and for the variance is

$$V[T_q | X(0) = x] = 8 \int_q^x s(\zeta) \int_\zeta^{+\infty} s(\xi) \left(\int_\xi^{+\infty} m(\theta) d\theta\right)^2 d\xi d\zeta. \quad (10)$$

3. Logistic model

In Braumann (1999) we can find such model with no Allee effects, in particular the classical logistic model, corresponding to $f(X) = r \left(1 - \frac{X}{K}\right)$, with intrinsic growth rate $r > 0$. A model of population growth with weak Allee effects similar to the logistic models is $f(X) = r \left(1 - \frac{X}{K}\right) \left(\frac{X}{E} + 1\right)$, with $0 < E < K$. In this case the growth rate is positive for $X < K$. For $X < L = \frac{K-E}{2}$ growth rate increases and for $X > L$ the growth rate decreases.

In a randomly varying environment, the growth rate will have a geometric average value $f(X)$ and random perturbations that we approximate by $\sigma\epsilon(t)$. The resulting stochastic differential equation of Stratonovich is

$$\frac{1}{X} \frac{dX}{dt} = r \left(1 - \frac{X}{K}\right) \left(\frac{X}{E} + 1\right) + \sigma\epsilon(t), \quad (11)$$

with $X(0) = x$ known. The solution $X(t)$ is a homogeneous diffusion process with drift coefficient

$$a(x) = \left(r \left(1 - \frac{x}{K}\right) \left(\frac{x}{E} + 1\right) + \frac{\sigma^2}{2}\right) x, \quad (12)$$

and diffusion coefficient

$$b(x) = \sigma^2 x^2. \quad (13)$$

The scale density is

$$s(y) = Cy^{-\frac{2r}{\sigma^2}-1} \exp\left(\frac{r}{\sigma^2 KE} (y^2 - 2y(K - E))\right) \quad (14)$$

and the speed density is

$$m(y) = \frac{1}{C\sigma^2} y^{\frac{2r}{\sigma^2}-1} \exp\left(-\frac{r}{\sigma^2 KE} (y^2 - 2y(K - E))\right), \quad (15)$$

with $C > 0$ constant.

The state space has boundaries $X = 0$ and $X = +\infty$ non-attracting and therefore, "mathematical" extinction has zero probability of occurring, explosion can not occur and the solution exists and is unique for all $t > 0$. As usual in dynamical systems, to reduce the number of parameters and work with adimensional quantities, let us consider $R = \frac{r}{\sigma^2}$, $d = \frac{q}{K}$, $z = \frac{x}{q}$ e $\gamma = \frac{E}{K}$. For the same reason, we will obtain expressions for the adimensional quantities $rE[T_q|X(0) = x]$ and $r^2V[T_q|X(0) = x]$. In particular, the expression for the mean of the first passage time is

$$rE[T_q|X(0) = x] = 2R \int_{\sqrt{\frac{R}{\gamma}d}}^{\sqrt{\frac{R}{\gamma}dz}} u^{-2R-1} e^{(u-\sqrt{\frac{R}{\gamma}(1-\gamma)})^2} \int_u^{+\infty} y^{2R-1} e^{-(y-\sqrt{\frac{R}{\gamma}(1-\gamma)})^2} dy du \quad (16)$$

and for the variance is

$$\begin{aligned} r^2V[T_q|X(0) = x] &= 8R^2 \int_{\sqrt{\frac{R}{\gamma}d}}^{\sqrt{\frac{R}{\gamma}dz}} u^{-2R-1} e^{(u-\sqrt{\frac{R}{\gamma}(1-\gamma)})^2} \int_u^{+\infty} v^{-2R-1} e^{(v-\sqrt{\frac{R}{\gamma}(1-\gamma)})^2} \\ &\quad \left(\int_v^{+\infty} y^{2R-1} e^{-(y-\sqrt{\frac{R}{\gamma}(1-\gamma)})^2} dy \right)^2 dv du. \end{aligned} \quad (17)$$

4. Conclusions

In this work we have studied general stochastic models with weak Allee effects describing populations growing in randomly varying environments. For these models, we have shown existence and uniqueness of the solution. Contrary to SDE strong Allee effects models, in SDE weak Allee effects models "mathematical" extinction has zero probability of occurring and there is a stationary density. "Realistic" extinction occurs with probability one and expressions for the mean of variance of the extinction time were obtained. We illustrated the results with a example, namely a model based on the classic logistic model.

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