Biomath Communications

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Allee Effects in Population Dynamics[1]

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Keywords: Population biology, Predator-prey, Beddington.

Introduction. The Allee effect is a phenomenon in biology characterized by a positive correlation between population density (size) and its per capita growth rate [1]. In their book, Courchamp et al [3], the authors described the Allee effect in a straightforward manner: "The more the merrier". This effect is simply a casual positive relationship between the number of individuals in a population and their "overall individual fitness." The more individuals there are, up to a point, the better they fare. So as population size approaches a threshold, favorable influences stimulate its growth, and when it goes below it, unfavorable influences inhibit its growth. From their point of view, the Allee effect may be described as a notion of positive density dependence in which the "overall individual fitness", or one of its components, is positively related to population size or density [3]. However, Lidicker [8] recently proposed that Allee effect may be described and defined in terms of demographic processes. He explained that "Allee effects are expressed at the population level of organization, and the parameters of interest are the population proponents of growth rates, recruitment rates, loss rates, equilibrium densities, and perhaps, success in establishing new populations."

Some authors make a distinction between strong Allee effect and weak Allee effect: a strong Allee effect refers to a population that exhibits a "critical size or density" below which population declines to extinction and above which it survives; while a weak Allee effect refers to a population that lacks a "critical density", but where, at lower densities, the population growth rate rises with increasing densities (Stephens et al [11], Lidicker [8])

Stephens et al [11] made the distinction between the component Allee effect, of particular interest to behaviorists, and the demographic Allee effect, of overriding concern to conservationists. From these authors' point of view, the benefits of conspecific presence may include one or more predator dilution or saturation; antipredator vigilance or aggression; cooperative

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[1] An invited talk given during BIOMATH 2014.

Citation: Ufuktepe, Ü.: Allee Effects in Population Dynamics. Biomath Communications 1/1 (2014), 12–19. `http://dx.doi.org/10.11145/j.bmc.2014.08.012`

predation or resource defense, social thermoregulation; collective modification or amelioration of the environment; increased pollination or fertilization success, conspecific enhancement of reproduction, and reduction of inbreeding, genetic drift, or loss of integrity by hybridization. Stephens et al [11] then put forward a definition of the Allee effect as follows: "The Allee effect is defined as a positive relationship between any component of individual fitness and either numbers or density of conspecifics."

Allee et al [1] provided experimental and field studies that confirmed the presence of the Allee effect among many species. The examples include bobwhite quails (*Colinus virginianus*) that huddle together to lower the surface presented to cold weather, and the disappearance of tsetse fly from an area in which the density of the flies fall below a threshold minimum density. Allee [1] himself considered two types of Allee effect and observed the Allee effect caused by reduction in the number of mice, and the Allee effect caused by reduction in density of flour beetles, *Tribolium confusum*. In [11], Stephens and Sutherland described several scenarios that cause the Allee effect in both animals and plants. For example, cod and many freshwater fish species have higher juvenile mortality when there are fewer adults. While fewer red sea urchin give rise to worsening feeding conditions of their young and less protection from predation. In some mast flowering trees, such as *Spartina alterniflora*, with a low density have lower probability of pollen grain finding stigma in wind-pollinated plants. The Allee effect may explain one of the most dramatic extinctions of modern times—that of the passenger pigeon *Estopistes migratorius* [11].

Model Derivation for Single Species. Let x_t be the population density of generation t, and $f(x_t)$ be the per-capita growth rate of the population. Then the dynamics of populations with synchronized generations are described by the difference equation

$$x_{t+1} = x_t f(x_t) \tag{3}$$

Allee effect occurs when the per-capita growth rate increases at low densities, that is $f'(x) > 0$ for x sufficiently small. A strong Allee effect occurs if in addition to the above assumption, there is a positive equilibrium density A such that the per-capita growth rate $f(x)$ is less than one if $x < A$ and greater than one for some densities greater than A. As stated by Schreiber [10], the dynamics of (1) with a strong Allee fall generically into two categories:

Bistability: if a population initiated at the maximal density M exceeds the critical density A in the next generation (i.e. $Mf(M) > A$), then there is an interval of initial population densities for which the population persists.

Essential extinction: if a population initiated at M falls below A in the next generation (i.e. $Mf(M) < A$), then for almost every initial population density extinction occurs." Screiber [10], then proposed that for species that possess the strong Allee effect, the per-capita growth rate function $f(x_t)$ can be viewed as the product of two functions, $f(x_t) = g(x_t). \ I(x_t)$, where $g(x_t)$ represents a negative density factor and $I(x_t)$ represents a positive density factor. In the absence of Allee effect, $I(x_t) = 1$. Thus $g(x_t)$ is the per-capita growth rate of the population in the absence of the Allee effect and may be one of the various functions that describe the dynamics of single species, such as the Ricker model, the Beverton-Holt model, the logistic model, the Hassell model, etc. Many authors [7], [4], [10] classify the Allee effect factors into two categories: (i) Allee effects caused by predator saturation and (ii) Allee effects caused by mate limitation. For the Allee effect due to predator saturation, we let $I(x) = \exp(-\frac{m}{1+sx})$ be the probability of escaping predation by a predator with a saturating functional response where m represents predation intensity and s is the proportional to the handling time (Hassell et al). For instance, if one uses the Ricker model, the difference equation (1) becomes

$$x_{t+1} = x_t \exp(r(1 - \frac{x_t}{k}) - \frac{m}{1 + sx_t}), \tag{4}$$

the Beverton-Holt model becomes

$$x_{t+1} = \frac{\mu k x_t}{k + (\mu - 1)x_t} e^{\frac{-m}{1 + sx_t}}, \tag{5}$$

and the Hassell model becomes

$$x_{t+1} = \frac{r x_t}{(1 + kx_t)^b} \cdot e^{\frac{-m}{1 + sx_t}}. \tag{6}$$

Allee effects may be caused by the difficulty of finding mates at low densities. For instance, in a field experiment, Levitan et all found 0% of a small dispersed group of sea urchins *Strongylocentrotus franciscanus* were fertilized, while an 82.2% fertilization rate twas reported in the center of a large aggregated group of sea urchins. to model mate limitation, we let $I(x) = \dfrac{sx}{1 + sx}$ be the probability of finding a mate where s is an individual's searching efficiency (Dennis 1989 [5] ,Scheuring 1999 [9]). Hence the Ricker model becomes

$$x_{t+1} = x_t \exp(r(1 - \frac{x_t}{k}) \cdot \frac{sx_t}{1 + sx_t}, \tag{7}$$

the Beverton-Holt model becomes

$$x_{t+1} = \frac{\mu k x_t}{k + (\mu - 1)x_t} \cdot \frac{sx_t}{1 + sx_t}, \tag{8}$$

and the Hassell model becomes

$$x_{t+1} = \frac{r x_t}{(1 + kx_t)^b} \cdot \frac{sx_t}{1 + sx_t}. \tag{9}$$

Brashares et al [2] identified the Vancouver Island Marmot as an endangered species that is on the brink of extinction. This large rodent is geographically restricted to Vancouver Island and evolved rapidly after its arrival after glacial retreat 10,000 years ago. The authors provided evidence of the presence of the Allee effect in this population by exhibiting the graph of data, where the x-axis represents the population size x_t and the y-axis represents the logarithm of per-capita growth rate $\ln \frac{x_{t+1}}{x_t}$.

It is evident that the per-capita growth rate is below one $(\ln \frac{x_{t+1}}{x_t} < 0)$ when the population size increases and reaches a threshold size (Allee equilibrium, point A) $(\log(\frac{x_{t+1}}{x_t}) = 0)$. The per-capita growth rate keeps increasing but a certain critical size (around 200 marmots) [2] the curve turns downward, with a decreasing reproductive rate. The authors hypothesize that the marmots have increased their range due to a lack of mates nearby. Thus the very process of increasing their per-capita growth rates is hindered because they cannot find mates, and when they go looking, are more likely to be killed by predators or get lost in unfamiliar territory.

Definition 1. Model (1) is said to have a strong Allee effect if the following conditions hold true.

(i) $f'(x) > 0$ for $x \in (o, \epsilon)$, for some $\epsilon > 0$,
(ii) $f(0) < 1$,
(iii) There exists a unique $k > 0$ such that $f(k) = 1$ and $f'(k) < 0$.

Note that from the above conditions one concludes that there exists an equilibrium point A, $0 < A < k$, such that $f(A) = 1$ and A is unstable.

Elaydi and Sacker [6] used the following rational function as the per-capita growth rate

$$f(x) = \frac{ax + r}{x^2 + cx + d}$$

to model the strong Allee effect and hence the model is given by

$$x_{t+1} = \frac{ax_t^2 + rx_t}{x_t^2 + cx_t + d} \tag{10}$$

This model is a variation of the Beverton-Holt model with an Allee effect caused by mate limitations as in (5).

Forcing the graph of $f(x)$ to pass through the three points in Figure 2 we obtain

$$f(x) = \frac{(A + k + c)x + \frac{RAk}{1 - R}}{x^2 + cx + \frac{RAk}{1 - R}}$$

Using this $f(x)$ one may conclude that for large x, $xf(x)$ is asymptotic to $A+k+c$.

We now point out the differences between model (6) and the other models (2, 3, 4, 5). Now in models (2) and (4) of the Ricker-type large overstocking leads to extinction, while in models (3) and (5) of the Beverton-Holt type, with overstocking, the population goes tot the stable equilibrium k. In Model (6), however, the parameter c controls the outcome of overcompensation, which will call the shock recovery parameter. If $c = -(A+k)$, then large overcompensation would lead to the extinction of the population. Moreover, if $c > -k$, then overstocking does not lead to extinction and the population returns towards the interior stable equilibrium k.

In this proposal we will focus our attention in the Hassell model given by

$$x_{t+1} = \frac{rx_t}{(1+kx_t)^b}$$

where we have undercompensation if $0 < b < 1$, exact compensation if $b = 1$ and overcompensation if $b > 1$. We will investigate the Hassell model with the Allee effect caused by either predator saturation or caused by mate limitation. Fowler and Ruxton studied the Hassell model with the Allee effect but using an Allee function $I(x)$ that was not biologically justified.

Model derivation for 2-species. We now extend single-species models with Allee effects to two-species/two-dimensional population models. and a non-extinction region separated by an Allee curve (curves).

Model derivation for 2-species predator-prey. Nicholson and Bailey [18] developed a general host-parasite model that is still the basis for most recent studies. Let H_t be the density of the host (prey) at time t and P_t be the density of the parasite (predator) at time t. Then the model is given by

$$H_{t+1} = rH_t f(H_t, P_t),\ P_{t+1} = eH_t(1 - f(H_t, P_t)), \tag{11}$$

where $f(H_t, P_t)$ is the fraction of hosts not parasitized, r is the number of eggs laid by a host that survives through the larvae, pupae, and adult stages, and e is the number of eggs laid by a parasitoid on a single host that survive through larvae, pupae, and adult stages. Based on the assumption that the host-parasite encounter is random and follows the Poisson distribution, Beddington and Bailey purposed that $f(H_t, P_t) = e^{-aP_t}$, where a represents the searching efficiency of the parasite. Then (10) becomes

$$H_{t+1} = rH_t e^{-aP_t}, P_{t+1} = eH_t(1 - e^{-aP_t}). \tag{12}$$

Unfortunately, this model is unrealistic since in the absence of the parasite the host grows exponentially. This is due to the fact that the model is density dependent.

In 1975, Beddington et al modified the latter model by adopting the single species density-dependent Ricker model as follows

$$H_{t+1} = H_t e^{r(1-\frac{H_t}{k})-aP_t}, P_{t+1} = H_t(1-e^{-aP_t}), \tag{13}$$

where k is the carrying capacity of the host. With the Allee effect caused predator saturation (12) becomes

$$H_{t+1} = H_t e^{r(1-\frac{H_t}{k})-aP_t} - \frac{m}{1+sH_t}.P_{t+1} = eH_t(1-e^{-aP_t}) \tag{14}$$

Alternatively, with the Allee effect caused by mate limitation, equation (14) becomes

$$H_{t+1} = H_t e^{r(1-\frac{H_t}{k})-aP_t} \cdot \frac{sH_t}{1+sH_t} \tag{15}$$

$$P_{t+1} = eH_t(1-e^{-aP_t})$$

Of course, one may use alternatively any of the single-species models instead of the Ricker model. S. Jang [7] used the Beverton-Holt model in her study of the host-parasitoid model with the Allee effect.

Summary. In this project we will examine the Host-parasite models with the Allee effect using the Ricker, the logistic, and Hassell models.

In both competition and predator-prey models we are going to investigate the following items:

1. Local and global stability analyzed of the equilibrium and periodic points;
2. Invariant manifolds: center, stable, and unstable;
3. Bifurcation: saddle-node, period-doubling, and Neimark-Sacker;
4. Parameter-space bifurcation diagrams that show the stability region in the parameter space;
5. Biological conclusions.

Recently, new tools to determine the global dynamics of planar discrete dynamical systems have been developed by Elaydi and his collaborates [17]. These tools include the use of singularity theory developed in the last century by Hassler Whitney [15]. Other important tools in the theory of critical curves were introduced by Mira and his collaborates [16].

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