

MATING STRATEGIES AND THE ALLEE EFFECT: A COMPARISON OF MATHEMATICAL MODELS

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Population models are developed that incorporate three breeding strategies. The presence of Allee effects and the strength of such effects are shown to be dependent on breeding strategy. For each model it is shown what constraints on the parameters lead to unconditional extinction and what constraints allow survival. Two of the three models exhibit Allee effects for all parameter choices. For intermediate choices of parameter, one of these two displays unconditional extinction while the other exhibits conditional survival. For suitable choice of parameters, the third strategy shows no Allee effect at all. Comparison of the Allee basins demonstrates the advantages of behavioral adaptations that modify breeding strategies when the population falls in a critical region.

1. Introduction

In 1954, Allee hypothesized that a species may become extinct when its numbers fall below a particular threshold, [1]. This phenomenon, now known as the Allee effect, has been invoked to explain the decline populations of plants ([2], [3], [4]) birds ([5]) and marine organisms ([6],[7]) as well as mammals ([8]).

Researchers have postulated many mechanisms for the Allee effect, ranging from the difficulty of finding mates at low populations ([9],[10]). In this paper we investigate the hypothesis that breeding strategies that make it easier to locate a mate reduce the severity of the Allee effect.

Usually discussions about evolutionary “advantage” center on the notion of competition for resources. In this paper we are looking at a different kind of advantage, namely resilience of a population to shocks. A population

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that is at a stable equilibrium may suffer a reduction in numbers due to some unusual event. If the population is subject to an Allee effect, the shock may be enough to push the population into the basin of the attractor at the origin, the “Allee basin” as we shall call it, resulting in eventual extinction of the population. The type of mating strategy used by the population affects how large this basin is and therefore affects the ability of the population to withstand shocks. The size of the Allee basin essentially quantifies the advantage one strategy has over another in protecting the population from extinction due to sudden reduction in numbers.

Section 2 of this paper provides some useful background and references for the Allee effect and describes the software used for simulations. Section 3 introduces three different models incorporating mating strategies reflecting three different sets of assumptions. Sections 4, 5 and 6 analyze each of the three models separately. Section 7 compares the three mating strategies expressed by these models against one another. Section 8 summarizes the conclusions of the study.

2. Background

Both the Allee effect and the mechanisms described above are amenable to mathematical modeling. There is a large literature of single species models that use various growth rate terms reflecting a variety of assumptions but that do not distinguish populations of males and females. In many of these models an extinction threshold is built directly into the growth equation ([11],[12],[13],[14],[15],[16],[17],[18],[19]). Not surprisingly, these models exhibit an Allee effect which drives populations below this threshold to zero. Building the threshold directly into the model, however, does not elucidate the mechanism offered to explain the effect. Other single population models exhibit an Allee effect without explicitly building in a threshold below which growth rate is always negative ([20],[21],[22],[23]). All of these models use a growth rate that is a sum of at least two terms, one of which is negative. Mathematically, this change effectively separates the processes of birth and death. For population values where the birth rate drops below the death rate, populations decline. Thus one can calculate which parameters give an Allee effect in these models and also the value of the threshold for a given set of parameters. Again, because these are single population models, they cannot test explanations given in terms of mating, size of predator population, or other interactive scenarios.

One class of models attempts to address mating issues with sin-

gle population models incorporating various forms of mating probability ([24],[25],[26],[27],[28],[29],[30],[31], [32]). All of these models assume that the population of males is a fixed proportion of the female population, in order to reduce the problem to a single population.

In the study that follows, BGODEM software (Reid, 2008) was used to produce the time series graphs, Maple software produced the phase plane attractor basins, and Adobe Photoshop was used to superimpose Maple plots and find the basin boundaries.

3. A comparative study of mating

In this paper we will compare three models for population growth in the presence of a particular mating strategy. Each model is two dimensional, incorporating male and female populations separately. All models assume that males and females are in competition for resources.

3.1. Model 1: probabilistic mating

The first model uses a probabilistic form for mating that reflects the assumption that the act of mating as a strictly probabilistic event.

X=females, Y=males

$X' = (\text{growth constant}) * (\text{logistic regulator}) * (\text{female density}) * (\text{male density}) - (\text{death constant}) * (\text{female density})$

$Y' = (\text{growth constant}) * (\text{logistic regulator}) * (\text{female density}) * (\text{male density}) - (\text{death constant}) * (\text{male density})$

$$X' = a(1 - X - Y)XY - bX \quad (1)$$

$$Y' = a(1 - X - Y)XY - bY \quad (2)$$

Model 1 assumes little agency on the part of the organism, as for example is the case with wind pollinated plants.

3.2. Model 2: completely efficient monogamous mating

In the second model we assume that males and females do not have to work to find one another. All possible mating pairs are formed in what

4

is assumed to be a monogamous fashion. The probabilistic term $X*Y$ is therefore replaced by the number of potential pairs, $\min(X,Y)$.

X =females, Y =males

X' = (growth constant)*(logistic regulator)*(number of potential pairs)
- (death constant)*(female density)

Y' = (growth constant)*(logistic regulator)*(number of potential pairs)
- (death constant)*(male density)

$$X' = a(1 - X - Y)(\min(X, Y)) - bX \quad (3)$$

$$Y' = a(1 - X - Y)(\min(X, Y)) - bY \quad (4)$$

Model 2 is completely efficient but relies equally on the presence of males and females. Monogamous species living in high density groups, where no searching is required to find a mate, would be an example of the behavior reflected in model 2.

3.3. Model 3: partially efficient probabilistic mating

The third model is for situations where the reproductive value of the female has more effect on the growth rate, with the utility of the males approaching 1 at a low percentage of the carrying capacity. This model still has a probabilistic aspect, but assumes a type of mating behavior, such as polygamy, which allows a small number of males to encounter many females. We use a Holling term for the male contribution:

$$\text{Male utility} = U(Y) = Y/(c + Y)$$

Notice that the ratio approaches 1 as Y goes to infinity, and is zero when Y is zero. Choosing $c = .01$, for example, gives $U(.1) = 10/11$, very close to 1 at only ten percent capacity for Y . The constant c is called the “half saturation” constant because when $Y = c$ the utility U equals one half (of the maximum possible utility, which is 1). Note also that, as Y approaches zero, the term $Y/(c + Y)$ representing male utility is $O(Y/c)$, giving a growth rate near zero of a/c . Thus a low proportion of males in the population can effectively serve as many females as are available, and the marginal utility of further males is low. As c approaches zero the model approaches one in which the birth rate only depends on the number of females and the available resource. Thus c describes a range of probabilistic

mating behaviors in which the encounter rate is disproportionately large at low male population sizes. We will call this model “partially efficient probabilistic mating”.

X=females, Y=males

$X' = (\text{growth constant}) * (\text{logistic regulator}) * (\text{female density}) * (\text{male utility}) - (\text{death constant}) * (\text{female density})$

$Y' = (\text{growth constant}) * (\text{logistic regulator}) * (\text{female density}) * (\text{male utility}) - (\text{death constant}) * (\text{male density})$

$$X' = a(1 - X - Y)XY/(c + Y) - bX \quad (5)$$

$$Y' = a(1 - X - Y)XY/(c + Y) - bY \quad (6)$$

In the next three sections we give the basic mathematical results for each of these models.

4. Analysis of model 1:

$$X' = a(1 - X - Y)XY - bX \quad (7)$$

$$Y' = a(1 - X - Y)XY - bY \quad (8)$$

The Jacobian for this system is given by

$$\begin{pmatrix} aY - 2aXY - aY^2 - b & aX - aX^2 - 2aXY \\ aY - aY^2 - 2aXY & aX - 2aXY - aX^2 - b \end{pmatrix}.$$

At extinction, the value $(0, 0)$ gives a diagonal Jacobian, with eigenvalues $-b, -b$. By the Hartman-Grobman theorem (Hartman, 1960), extinction is always an attracting state for this system. Therefore if survival of the species is possible, it is always conditional on the size of the populations of males and females. That is, the Allee effect is always present. Solving for critical points other than $(0, 0)$, we get the solutions

$$X = Y = (1/2)(1 + \sqrt{(1 - 8b/a)}) \quad (9)$$

and

$$X = Y = (1/2)(1 - \sqrt{(1 - 8b/a)}) \quad (10)$$

From these we see that survival, which requires critical points with positive real values, is only possible if $a > 8b$. That is, the inherent growth rate must be eight times the natural death rate for the species to be viable. Furthermore, when $a > 8b$ at one of the critical points X and Y are both greater than .5, and at the other critical point they are both less than .5. In the following discussion we assume $a > 8b$. Note that with strict inequality there will be no repeated roots.

Computing the Jacobian at $X = Y$ and using the relation $X^2 = (aX - b)/(2a)$ gives a Jacobian $J(T)$ of the form:

$$\begin{pmatrix} aT & T + b \\ T + b & T \end{pmatrix}.$$

Where

$$T = -(a/2)X + b/2 \quad (11)$$

Notice that T is a real number.

Computing the eigenvalues of J is straightforward and yields $(2T + b, -b)$. For $X > 1/2$ and $a > 8b$, we have

$$2T + b = -aX + 2b < -a/2 + 2b = (-a + 4b)/2 < 0 \quad (12)$$

Thus by the Hartman-Grobman theorem this is an attracting fixed point. Thus, sufficiently large populations will reach a nontrivial equilibrium. Figure 1 shows a typical simulation of this system with starting populations large enough to avoid the Allee effect.

If we make the common assumption (which Figure 1 demonstrates is not justified) that the male population is a constant proportion of the female population, $Y = mX$, we get the single population system studied in Aviles (1999)

$$X' = a(1 - (1 + m)X)X^2 - bX \quad (13)$$

The basin of attraction for the trivial fixed point, hereafter called the Allee basin, is shown for several choices of constant in Figure 2.

As the inherent growth rate, a , decreases, the basin grows. The fixed points corresponding to conditional survival are shown along with the

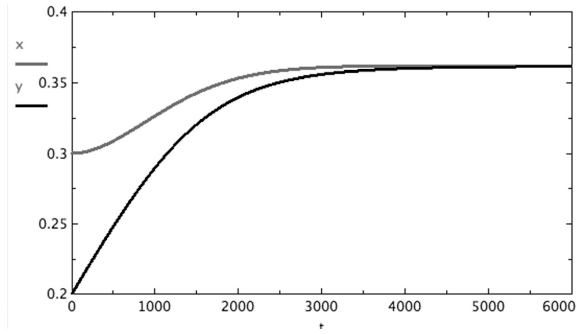


Figure 1. Model 1, with $b = .001$ and $a = .01$

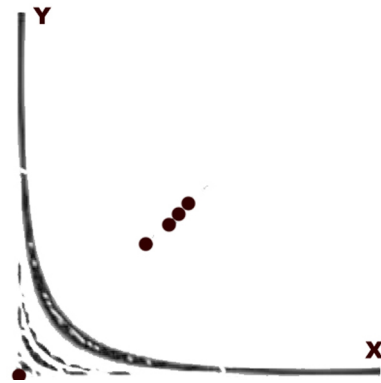


Figure 2. Model 1, with $b = .001$ and $a = .01, .015, .02, .04$

boundaries for the basins of attraction. Note that the largest basin corresponds to the lowest fixed point.

5. Analysis of model 2:

$$X' = a(1 - X - Y)(\min(X, Y)) - bX \tag{14}$$

$$Y' = a(1 - X - Y)(\min(X, Y)) - bY \tag{15}$$

In this situation the function $\min(X, Y)$ is not differentiable. However, it is always equal to the simple function X or Y , depending on which is

greater. So we will investigate the dynamics of these two simple systems, each of which represents the behavior of the system on half of the phase space. For ease of discussions we will refer to the following two systems:

System 1, valid for $X > Y$:

$$X' = a(1 - X - Y)Y - bX \quad (16)$$

$$Y' = a(1 - X - Y)Y - bY \quad (17)$$

System 2, valid for $X < Y$:

$$X' = a(1 - X - Y)X - bX \quad (18)$$

$$Y' = a(1 - X - Y)X - bY \quad (19)$$

We can also consider

System 3, valid for $X = Y$:

$$X' = a(1 - 2X)X - bX \quad (20)$$

For both systems 1 and 2 we obtain fixed points at $(0, 0)$ and $X = Y = .5 - b/(2a)$. The second fixed point will be in the positive quadrant if $a > b$. Computing the Jacobians for systems 1 and 2 and the relevant derivative for system 3 we have:

$$J(\text{system1}) = \begin{pmatrix} -aY - b & a - aX - 2aY \\ -aY & a - aX - 2aY - b \end{pmatrix}.$$

$$J(\text{system2}) = \begin{pmatrix} a - aY - 2aX - b & -aX \\ a - aY - 2aX & -aX - b \end{pmatrix}.$$

$$J(\text{system3}) = a - 4aX^2 - b$$

At the critical point $(0, 0)$, the eigenvalues for systems 1 and 2 are $-b$ and $a - b$, whereas the value of the Jacobian for system 1 is $a - b$. Thus if $a < b$, the equilibrium at $(0, 0)$ is attracting, as all of these values are

negative. However if $a > b$, the eigenvalues have mixed signs. Because this model is really three different systems in the regions $X > Y$, $X < Y$ and $X = Y$ we cannot say automatically whether extinction is an attracting state or not. However if we look at the value of Y near the origin for system 1, we have

$$Y' = a(1 - X - Y)Y - bY = Y(a(1 - X - Y) - b) = Y(a - b - a(X + Y)) \quad (21)$$

Thus if $X + Y$ is sufficiently small and $a > b$, we see that $Y' > 0$.

We have shown that near the origin, as long as Y does not equal 0, the flow always has a component in the Y direction away from $(0, 0)$ in system 1. For the situations where $Y > X$ in system 2 and $Y = X$ in system 3, a similar calculation shows that $X' > 0$ for X sufficiently small. So this system does not display an Allee effect for $a > b$. The assumption that males are a constant proportion of females yields a version of the logistic equation, displaying unconditional survival or extinction depending on choices of a, b , and the constant of proportionality chosen.

For model 2 there is a second fixed point when $a > b$, given by $X = Y = 1/2 - b/(2a)$. The Jacobian for system 1 representing this model may be evaluated at this value to give eigenvalues of $-b$ and $-(a + 3b)$. The Jacobian for system 2 is just the inverse transpose of that of system 1 and thus has the same eigenvalues. The Jacobian of system 3 is the second of these eigenvalues. All are negative. Invoking Hartman-Grobman for each of these systems, and noting that our model is always equivalent to one of the three on every region of the phase plane, we can conclude that the nonzero equilibrium is indeed an attracting state. To summarize, model 2 displays unconditional extinction if $a < b$ and unconditional survival when $a > b$.

6. Analysis of model 3:

$$X' = a(1 - X - Y)XY/(c + Y) - bX \quad (22)$$

$$Y' = a(1 - X - Y)XY/(c + Y) - bY \quad (23)$$

In these equations all parameters are positive and $c < 1$.

Besides the equilibrium at $(0, 0)$, these equations also yield fixed points when $Y = X$ at

10

$$X = Y = ((a - b) + \sqrt{((a - b)^2 - 8abc)})/4a \quad (24)$$

and

$$X = Y = ((a - b) - \sqrt{((a - b)^2 - 8abc)})/4a \quad (25)$$

Several things are evident from this expression. If $a < b$, the only fixed point of the system is $(0, 0)$. There will be real roots only when $(a - b)^2 > 8abc$. In this case the roots will both be positive when $a > b$. Henceforth for this model we assume that a , b and c fall into this range. The Jacobian of the system is given by

$$\begin{pmatrix} \frac{aY}{(c+Y)}(1 - 2X - Y) - b & \left(\frac{-aXY}{(c+Y)} + \frac{a(1-X-Y)Xc}{((c+Y)^2)} \right) \\ \frac{aY}{(c+Y)}(1 - 2X - Y) & \left(\frac{-aXY}{(c+Y)} + \frac{a(1-X-Y)Xc}{((c+Y)^2)} - b \right) \end{pmatrix}.$$

At $(0, 0)$ the Jacobian is diagonal with both eigenvalues equal to $-b$. Thus the origin is an attracting fixed point and the system displays the Allee effect for all parameters.

We now turn to the computation of stability of the larger nonzero fixed point. It suffices to show that the determinant of the Jacobian at this point is positive and its trace is negative.

Computing the trace of the Jacobian matrix under the constraints for the nonzero fixed points given by

$$0 = a(1 - 2X)X^2/(c + X) - bX \quad (26)$$

and

$$X = Y \quad (27)$$

yields an expression for the trace T at nonzero equilibrium X of

$$T(X) = 1/(c + X)^2(-b/2a)(X(a - b + 2ac) - bc) \quad (28)$$

Let

$$L(X) = (-b/2a)(X(a - b + 2ac) - bc) \quad (29)$$

Then $T(X) < 0$ if and only if $L(X) > 0$. The slope of the line given by the expression $L(X)$ is negative and it is easy to check that $T((a - b)/4a)$ is also negative.

To compute the determinant, we use the fact that at equilibrium $X = Y$ and X solves $2aX = (a - b)X - bc$ to reduce the Jacobian to a positive multiple of

$$\begin{pmatrix} -aX & a - 3X - b \\ a - 3X & -aX - b \end{pmatrix}.$$

Computing the determinant and plugging in the larger of the two nonzero equilibrium values gives the determinant as a positive multiple of the expression

$$2(a + b)\sqrt{(a - b)^2 - 8abc} - 2(a - b)^2 + 16abc \quad (30)$$

It is an easy exercise to show that this is positive under the assumptions on a, b, c given above.

The fixed point given by equation 24 is therefore stable. Thus if model 3 has positive fixed points other than the origin, at least one of them is stable. Survival of the population is conditional due to the Allee effect that is always present in this model. Figure 3 shows a typical simulation of the two populations of this model.

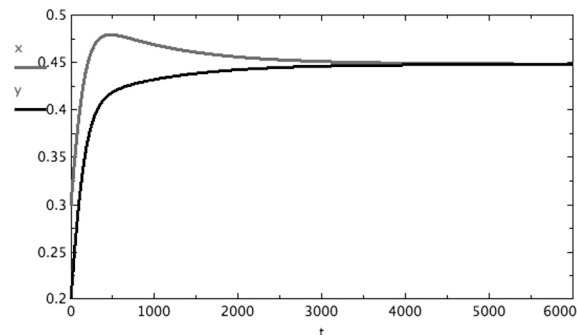


Figure 3. Model 1, with $b = .001$, $a = .01$ and $c = .0125$

Figure 4 shows the change in the Allee basin as the inherent growth rate, a is increased, while other parameters remain fixed.

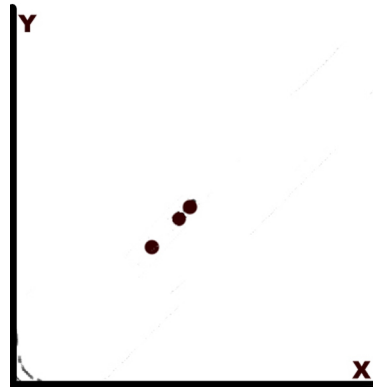


Figure 4. Model 3, with $b = .001$, $c = .0125$ and $a = .005, .01, .015$

If we assume that males are a constant proportion of females (which Figure 3 shows is not justified), we obtain the equation:

$$X' = ma(1 - X - mX)X^2/(c + mX) - bX \quad (31)$$

Note that in this case the lack of symmetry gives a different reduction if we start with the equation for Y' . In any case, this equation has been studied by Takeuchi (1996).

7. Comparison of three strategies

In all three models we have used a and b as birth and death parameters respectively. For model 1 (distributed monogamy) and model 3 (polygamy) we see that the Allee effect is always present. For model 1 a must be greater than $8b$ for conditional survival of the population, whereas for model 3, $a > b$ suffices although there is also a condition on the third constant. For model 2 (enhanced monogamy), $a > b$ is required for survival of the population, but if $a > b$ there is no Allee effect present. Notice that in all models a viable population tends to equal numbers of males and females, even in the “partially efficient mating” model. Figure 5 provides a visual description of the relative advantage of model 3 over model 1.

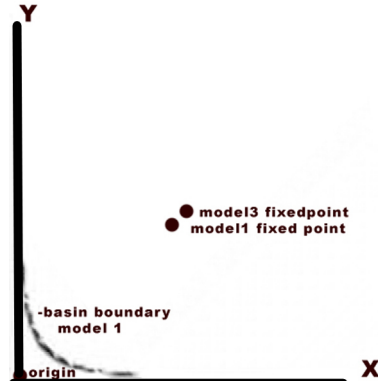


Figure 5. Models 1 and 3, with $b = .001$, $a = .01$ and $c = .0125$

In Figure 5 we see a visible Allee basin for model 1, whereas the Allee basin for model 3 is too small to be visible in the diagram.

The question addressed by this study is how a population with given mating dynamics responds to a shock to the system. A shock, for this purpose, is a sudden reduction of population. Suppose the population has reached its nonzero equilibrium and then experiences an instantaneous symmetric (in X and y) reduction in numbers. We would like to compare the maximal possible shock that the population could sustain and still be viable.

In both models 1 & 3 the diagonal distance from the nonzero stable equilibrium to the Allee basin boundary is just the distance between the two nonzero fixed points. The lower, unstable, nonzero fixed point sits on the Allee basin boundary. So the distance between the two nonzero fixed points is exactly the maximum possible shock the system can handle if the populations start at the stable equilibrium and are reduced equally in X and Y . We will call these distances MSS_1 and MSS_3 respectively, for "maximum symmetric shock"

$$MSS_1 = \sqrt{22}\sqrt{(1 - 8b/a)} \quad (32)$$

$$MSS_3 = \sqrt{22}\sqrt{((a - b)^2 - 8abc)}/4a \quad (33)$$

Figure 5 shows a typical run in which MSS_3 is greater than MSS_1 . In order for this to happen, it suffices to show that $MSS_3^2 - MSS_1^2 > 0$. A

calculation shows that this is equivalent to

$$3 + 4b^2/a^2 - 32bc/a > 0 \quad (34)$$

Recall that, in order for model 1 to have a stable nonzero equilibrium, it must be that $a > 8b$. Making this assumption it suffices to show that

$$3 + 4b^2/a^2 - 4c > 0 \quad (35)$$

The left expression will be positive for all a and b if $c < 3/4$. Remember that reducing c improves the efficiency of mating at low population levels. When $c = 1$ model 3 has no better reproduction rates than model 1 at low levels and does not represent any sort of improvement of efficiency. Our computer runs used $c = .0125$. We see then that model 3 is more resistant to shock than model 1 over a large range of biologically reasonable values for c , the parameter that controls the efficiency of the mating strategy.

8. Conclusions

The mating strategy an organism uses has a quantifiable effect on its ability to withstand reductions in number. We summarize the impact of mating strategies modeled in this paper below.

- (1) *The existence and strength of the Allee effect depend on mating strategies of the organism.* Comparison of models 1-3 shows that the Allee effect can disappear entirely or the size of the Allee basin can be reduced by the choice of mating strategy.
- (2) *Perfectly efficient mating eliminates the Allee effect (unless due to other causes).* Model 2 describes a situation where all mating pairs are utilized and exhibits no Allee effect when the birth rate exceeds the death rate.
- (3) *Partially efficient probabilistic mating strategies enhance the ability of a population to resist shocks.* Even when not terribly efficient, model 3 is more resistant to instantaneous symmetric reduction of its population, as measured by the diagonal distance from its stable nonzero fixed point to the Allee basin boundary.

These models raise interesting questions regarding interspecies competition in the presence of probabilistic mating strategies. In particular, running numerical experiments where a small number of organisms are introduced into an existing population of competitors (as is often the case in

nature) show inevitable extinctions of the introduced organism due to the Allee effect. That is, the introduced organism would die out whether the competitor was there or not. The outcome of multiple species models will look very different when mating strategies are included, suggesting many areas for future research.

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