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vol. 12, no. 8



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(Communicated by Kenneth S. Berenhaut)

We analyze a logistic two-sex model with mate-finding Allee effects assuming distinct sex-related parameters. We compute the threshold of the Allee-effect strength that separates population extinction from persistence and prove that a bistability regimen appears whereby the total population either goes extinct or stabilizes at a positive level depending on the initial demographic conditions. We show that this effect is the only possible outcome as far as the population limiting behavior is concerned. In addition, we compute the optimal female-sex probability at birth that maximizes this threshold.

1. Introduction

Mathematical population models are a compromise between realism and mathematical tractability. It is obvious that no model can fully resemble the complexity of population interactions (both human or from the animal world). On the other hand, the simplest possible models are not acceptable for long-term predictions. The classical example is given by the exponential model, which appears whenever the vital rates such as birth and death are constant:

$$\frac{dP}{dt} = rP,$$

where P is the total population at time t and r is the difference between a constant birth and death rate. Such a model will always predict an exponentially increasing population as long as births exceeds deaths. This results in completely unrealistic population sizes as t increases.

The most well-known improvement on this model is the logistic equation:

$$\frac{dP}{dt} = r\left(1 - \frac{P}{K}\right)P.$$
(1)

MSC2010: 92D25, 92D50.

Keywords: two-sex models, mate-finding Allee effect, bistability.

This model takes into account the fact that there are always factors present that limit the growth rate as the total population increases. Indeed the population cannot grow if it surpasses K in the equation above (also known as *carrying capacity*). Typically, these logistic effects are modeled by considering the mortality rate as an increasing function of the total population size. What that means in real life varies depending on the context. In the ecological models the logistic effect can mean the effect of finite resources such as food. In the human populations the same effect can mean anything which affects the population negatively in overcrowding situations (i.e., infectious diseases, competition for resources, conflicts and other limiting effects). Altogether, logistic effects are examples of a negative correlation between population growth rate and the total population size: the bigger the population size the lower the growth rate.

While logistic effects make perfect sense whenever the population reaches high levels, they should not have any effect when the population density is low. For example, in many models, the logistic mortality is modeled as an increasingly linear function in P:

logistic mortality =
$$\mu + bP$$
,

where μ denotes the natural mortality (without population-dependent limiting factors) and b > 0 is a technical term that controls how fast the mortality increases with *P*. It is important to always assume that *b* is a very small coefficient. Otherwise, the mortality will increase too fast for relatively small increases in *P*. Indeed, at low population values, in many situations, an opposite effect happens: the growth rate should increase with *P*. This is the core assumption of the Allee effect, which, by definition, means that the population growth rate is *positively* correlated with the total population size if this size is low. One typical explanation for this effect is geographical dispersal: if the density is low the opportunity for reproduction is rare and it increases if the population density increases.

To summarize, a logistic effect assumes that the population cannot grow past a certain maximum level (the logistic threshold) and the Allee effect *requires* a minimum population level for the growth to occur (the Allee threshold). Most researchers agree that in many ecosystems both assumptions should be present for a more realistic model. A simple modification of the logistic equation (1) is the following one found in [Courchamp et al. 2008], among many other proposed functional forms:

$$\frac{dP}{dt} = r\left(\frac{P}{A} - 1\right)\left(1 - \frac{P}{K}\right).$$

Notice that the population can only grow if A < P(t) < K. Should the population size drop below the Allee threshold A, the total population goes extinct. This phenomenon is called a *strong Allee effect* to separate it from the *weak Allee effect*

in which low population values cause an exceedingly lower growth rate but without causing extinction. For a more detailed description of various types of Allee effects in ecology see [Courchamp et al. 2008].

One particular type of Allee effect, which is the focus of this paper, is the *mate-finding Allee effect*. This effect is considered in two-sex population models. It assumes that, whenever an individual of one sex is actively looking for a mating partner, the scarcity of the population of the opposite sex induces a strong Allee effect. In other words, the reproduction is hindered by the low population level of the opposite sex. Consider a two-sex population where F and M denote the total population of females and males at time t. Assuming that the female is the mate-searching sex, the mating probability of a given female will be a function of the total male population p(M) with the properties

$$p(0) = 0$$
, $\lim_{M \to \infty} p(M) = 1$, and p increasing in M .

These assumptions reflect that, if M is small, the reproduction chance is also small, whereas, if M is large, the reproduction probability approaches 1. It is important to point out that the actual reproduction term also depends on other factors. The total male population p(M) is only the mate-finding Allee effect as part of the mating term. There are many explicit forms for p(M) considered in the literature; see again [Courchamp et al. 2008]. Here we focus on the form

$$p(M) = \frac{M}{M+\theta}.$$

Other possible forms, with the properties listed above, are

$$1 - e^{-M/\theta}$$
 and $\frac{M^d}{M^d + \theta}$ with $d > 1$.

The constant term $\theta > 0$ is a measure of the Allee-effect strength and it describes how low the male population should be in order to notice a significant drop in the mating probability. In other words, if θ is very small, the male population should be very small as well in order for p(M) to significantly drop below 1. A large θ indicates that the mating probability decreases faster as M decreases. As we will show in this paper, there exists a threshold θ^* above which the population always goes extinct.

A model containing this type of mate-finding Allee effect has been analyzed in [Berec et al. 2018] under the assumptions that the sex ratio at birth is even and that the background mortality rates of females and males are equal. In reality, these parameters are sometimes different. One example, discussed later in this article, is provided by some mosquito populations. Seasonal conditions exert an influence in the hatching stimuli for the eggs of mosquitoes (as shown in [Lounibos and Escher

2008]) which leads to uneven sex ratios. Variation in the sex birth ratios is observed in other species as well, including birds and mammals; see [Mondard et al. 1997; Weimerskirch et al. 2005].

In this article we improve the result from [Berec et al. 2018] by keeping all sex-related parameters distinct. The paper is structured as follows: in Section 2 we introduce the two-sex model with mate-finding Allee effect and provide its full stability analysis. We also compute the threshold of the Allee-effect strength θ that separates population persistence from extinction. In Section 3 we consider θ as a function of the female-sex probability at birth and compute its optimal value that maximizes it. We conclude the paper with some interpretations of these results in Section 4 and thoughts on possible avenues for future research in Section 5.

2. A two-sex model with mate-finding Allee effect

The logistic two-sex population model with mate-finding Allee effect that we consider is

$$\begin{cases} \frac{dF}{dt} = \beta \gamma_f \frac{FM}{M+\theta} - \bar{\mu}_f F, \\ \frac{dM}{dt} = \beta \gamma_m \frac{FM}{M+\theta} - \bar{\mu}_m M, \end{cases}$$
(2)

where:

• F and M are the female and male population sizes at time t.

• β is the per capita female birth rate when there is no mate-finding Allee effect (i.e., when *M* is large).

- γ_f and γ_m are the probabilities that a newborn is a female or male respectively. Hence, $\gamma_f + \gamma_m = 1$.
- θ is the strength of the mate-finding Allee effect.

• μ_f and μ_m are the background female and male mortality rates respectively, in the absence of logistic effects.

• $\bar{\mu}_f := \mu_f + b(F + M)$ and $\bar{\mu}_m := \mu_m + b(F + M)$ are the female and male logistic mortality rates as linear functions of the total population; b > 0 represents the strength of the logistic effect.

Remark. While model (2) assumes that the female is the mate-searching sex, the result we establish in this paper holds if the roles are reversed; i.e., the male being the mate-searching sex while the mate-finding Allee effect would be $F/(F + \theta)$. It is not necessary to analyze this scenario separately: one would simply interchange the subscripts f and m throughout the paper.

Consider also the following additional notation (which will be justified in the proof of the main result):

$$\theta^* := \frac{\gamma_m}{b} \Big[\beta \gamma_f - \mu_f + 2(\gamma_f \mu_m + \gamma_m \mu_f) - 2\sqrt{\gamma_f (\gamma_f \mu_m + \gamma_m \mu_f)(\beta - \mu_f + \mu_m)} \Big], \quad (3)$$

and

$$\mathcal{R}_f := \frac{\beta \gamma_f}{\mu_f}.$$

Since $1/\mu_f$ is the expected female lifetime without the logistic effects, \mathcal{R}_f can be interpreted as the maximum net female reproductive number (the expected female offspring per reproductive female during her lifetime).

We now state our main result:

Theorem 2.1. If $\mathcal{R}_f < 1$ or $\theta > \theta^*$ then the population goes extinct due to either low female reproductive ability or too high a mate-finding Allee effect. If $\mathcal{R}_f > 1$ and $\theta < \theta^*$ then there exist two positive equilibria: one unstable and the other one locally asymptotically stable. The total population either goes extinct if it drops to low levels or it approaches the stable equilibrium.

Proof. The Jacobian of model (2) is

$$J(F,M) = \begin{bmatrix} \frac{\beta \gamma_f M}{M+\theta} - \bar{\mu}_f - bF & \frac{\beta \gamma_f F}{M+\theta} - \frac{\beta \gamma_f F M}{(M+\theta)^2} - bF \\ \frac{\beta \gamma_m M}{M+\theta} - bM & \frac{\beta \gamma_m F}{M+\theta} - \frac{\beta \gamma_m F M}{(M+\theta)^2} - \bar{\mu}_m - bM \end{bmatrix}.$$

The model always admits an extinction equilibrium (0, 0) which is always locally stable since

$$J(0,0) = \begin{bmatrix} -\mu_f & 0\\ 0 & -\mu_m \end{bmatrix}$$

with two negative eigenvalues $-\mu_f$ and $-\mu_m$.

Consider now a positive equilibrium (F^*, M^*) with $P^* := F^* + M^*$. Notice that any positive equilibrium must satisfy

$$\frac{\beta \gamma_f M^*}{M^* + \theta} = \mu_f + bP^* \quad \text{and} \quad \frac{\beta \gamma_m F^*}{M^* + \theta} = \mu_m + bP^*.$$

Using these identities, the Jacobian evaluated at this steady state becomes

$$J(F^*, M^*) = \begin{bmatrix} -bF^* & \frac{\beta\gamma_f F^*}{M^* + \theta} - \frac{\beta\gamma_f F^* M^*}{(M^* + \theta)^2} - bF^* \\ \frac{\beta\gamma_m M^*}{M^* + \theta} - bM^* & -\frac{\beta\gamma_m F^* M^*}{(M^* + \theta)^2} - bM^* \end{bmatrix}$$

In a system of two differential equations, the necessary and sufficient condition for the local stability of a steady state is $\text{Trace}(J(F^*, M^*)) < 0$ and $\det(J(F^*, M^*)) > 0$.

It is easy to see that the trace of this matrix is always negative and its determinant is

$$\det(J(F^*, M^*)) = \frac{\beta F^* M^*}{(M^* + \theta)^3} [b(M^* + \theta)(\theta + \gamma_m P^*) - \beta \gamma_f \gamma_m \theta].$$

Hence the stability condition for any biologically feasible (positive) steady state is

$$b(M^* + \theta)(\theta + \gamma_m P^*) - \beta \gamma_f \gamma_m \theta > 0.$$
(4)

Concerning the existence of a positive steady state, first, notice that

$$F^* = \frac{\gamma_f \theta(\mu_m + bP^*)}{\gamma_m(\beta\gamma_f - \mu_f - bP^*)} \quad \text{and} \quad M^* = \frac{\theta(\mu_f + bP^*)}{\beta\gamma_f - \mu_f - bP^*}$$

Hence, to ensure they are positive, any feasible value for P^* must satisfy

$$P^* < \frac{\beta \gamma_f - \mu_f}{b}.$$
 (5)

However this requires $\beta \gamma_f - \mu_f > 0$, which is equivalent to $\mathcal{R}_f > 1$. Thus, if the opposite holds, i.e., $\mathcal{R}_f < 1$, then (0, 0) is the only equilibrium point.

From here on we assume $\mathcal{R}_f > 1$, i.e.,

$$\beta \gamma_f > \mu_f.$$

From

$$P^* = F^* + M^* = \frac{\gamma_f \theta(\mu_m + bP^*)}{\gamma_m(\beta\gamma_f - \mu_f - bP^*)} + \frac{\theta(\mu_f + bP^*)}{\beta\gamma_f - \mu_f - bP^*}$$

it follows, after some computations, that P^* must be a positive root of

$$f(P) := b\gamma_m P^2 + [b\theta - \gamma_m(\beta\gamma_f - \mu_f)]P + \theta(\gamma_f \mu_m + \gamma_m \mu_f)$$

and P^* must satisfy (5). Furthermore, the stability condition (4) can be rewritten in terms of P^* as

$$P^* > P_v := \frac{\gamma_m(\beta\gamma_f - \mu_f) - b\theta}{2b\gamma_m}.$$
(6)

Notice also that P_v is the *P*-coordinate vertex of the parabola f(P). Consider now the discriminant of f(P) as a function of θ :

$$g(\theta) := b^2 \theta^2 - 2b\gamma_m [\beta\gamma_f - \mu_f + 2(\gamma_f \mu_m + \gamma_m \mu_f)]\theta + (\beta\gamma_f - \mu_f)^2 (\gamma_m)^2.$$

The discriminant of $g(\theta)$ is

$$16b^2\gamma_f(\gamma_m)^2(\gamma_f\mu_m+\gamma_m\mu_f)(\beta-\mu_f+\mu_m).$$

Under our current assumptions, this is positive since

$$\beta > \beta \gamma_f > \mu_f.$$

Taking into account the signs of the coefficients of $g(\theta)$ we conclude that $g(\theta)$ has two positive roots θ_1 and θ_2 :

$$\theta_1 = \frac{\gamma_m}{b} \Big[\beta \gamma_f - \mu_f + 2(\gamma_f \mu_m + \gamma_m \mu_f) - 2\sqrt{\gamma_f (\gamma_f \mu_m + \gamma_m \mu_f)(\beta - \mu_f + \mu_m)} \Big],$$

$$\theta_2 = \frac{\gamma_m}{b} \Big[\beta \gamma_f - \mu_f + 2(\gamma_f \mu_m + \gamma_m \mu_f) + 2\sqrt{\gamma_f (\gamma_f \mu_m + \gamma_m \mu_f)(\beta - \mu_f + \mu_m)} \Big].$$

Hence, $g(\theta)$ is positive whenever $0 < \theta < \theta_1$ and $\theta_2 < \theta < \infty$. From the sign of the coefficients of f(P) it is clear that, if f(P) has real roots, they are either both negative or both positive. They are positive provided that

$$\theta < \frac{\gamma_m}{b} (\beta \gamma_f - \mu_f)$$

However a straightforward computation shows that

$$g\left(\frac{\gamma_m}{b}(\beta\gamma_f - \mu_f)\right) = -4(\gamma_m)^2(\beta\gamma_f - \mu_f)(\gamma_f\mu_m + \gamma_m\mu_f) < 0,$$

which means

$$\theta_1 < \frac{\gamma_m}{b} (\beta \gamma_f - \mu_f) < \theta_2.$$

This shows that the model (2) admits two positive equilibrium points (F_1, M_1) and (F_2, M_2) corresponding to the two positive roots $P_1 < P_2$ if and only if the mate-finding Allee-effect strength θ is less than the threshold

$$\theta^* := \theta_1 = \frac{\gamma_m}{b} \Big[\beta \gamma_f - \mu_f + 2(\gamma_f \mu_m + \gamma_m \mu_f) - 2\sqrt{\gamma_f (\gamma_f \mu_m + \gamma_m \mu_f)(\beta - \mu_f + \mu_m)} \Big].$$
(7)

If $\theta > \theta^*$ then the extinction equilibrium (0, 0) would be the only steady state. Notice also that P_1 and P_2 , when they exist and are positive, both satisfy the feasibility condition $P^* < (\beta \gamma_f - \mu_f)/b$ since

$$f\left(\frac{\beta\gamma_f - \mu_f}{b}\right) = \theta\gamma_f(\beta - \mu_f + \mu_m) > 0,$$

$$f'\left(\frac{\beta\gamma_f - \mu_f}{b}\right) = \gamma_m(\beta\gamma_f - \mu_f) + b\theta > 0,$$

which means $P_1 < P_2 < (\beta \gamma_f - \mu_f)/b$.

Furthermore, $P_1 < P_v < P_2$, which means (F_1, M_1) is unstable and (F_2, M_2) is locally asymptotically stable. Thus we have bistability between the extinction and the positive steady state (F_2, M_2) .

It remains now to show that the asymptotic behavior established in this proof holds in the global sense and not just within an unspecified basin of attraction of each locally stable steady state. In other words, we want to show that, regardless of the initial population size, the population converges to either (0, 0) or (F_2, M_2) . In the case of a planar system, the only other possible limiting behavior is that of a limit cycle or, more generally, a finite number of equilibria cyclically chained. We show that this is not possible for our model (2).

First notice that it is not possible to have the extinction equilibrium (0, 0) as part of a group of equilibrium points that are cyclically chained. This is because (0, 0)is a sink (i.e., both eigenvalues are real and negative). Any other possible cycle would be entirely contained in a compact subset of the positive quadrant. We rule out also this possibility using the Dulac criterion [Perko 1991]. It states that if

$$\frac{\partial}{\partial F}(\varphi(F,M)F') + \frac{\partial}{\partial M}(\varphi(F,M)M')$$

has a constant sign on that compact subset for some differentiable function $\varphi(F, M)$ then the system (2) does not have any periodic solutions or limit cycles. A typical choice for the Dulac function is $\varphi(F, M) = 1/(FM)$. Indeed, in our case, this leads to

$$\frac{\partial}{\partial F}\left(\frac{1}{FM}F'\right) + \frac{\partial}{\partial M}\left(\frac{1}{FM}M'\right) = -\frac{1}{FM}\left[\frac{\beta\gamma_m FM}{(M+\theta)^2} + b(F+M)\right] < 0. \quad \Box$$

3. Maximization of the Allee-effect strength

As mentioned earlier, the model (2) has been analyzed in [Berec et al. 2018] using equal sex-related parameters. In this section we illustrate the advantage of keeping these parameters distinct whenever the biological question under study is specific to one sex only. To this end, we can see that the threshold θ^* can be analyzed further for various optimal scenarios. For example, if population persistence is a desired objective, then a natural question to ask is what combinations of parameters will maximize θ^* . Based on our results, a larger threshold θ^* means that the population may persist for relatively stronger Allee effects. One will still have bistability between extinction and persistence but, as long as $\theta < \theta^*$ and the population size is not too low to begin with, the long-term outcome is persistence. For example, it is easy to see that whenever μ_f approaches zero then, unsurprisingly, the threshold θ^* is maximized. When we analyze other parameters, the optimal combination that maximizes θ^* is less obvious. As an example, we compute in this section the female-sex probability at birth (γ_f) that maximizes θ^* for a numerical case. We will provide a more general result for a simplified version of θ^* .

Theorem 3.1. If $\mathcal{R}_f > 1$ there exists an optimal female-sex probability at birth, γ_f , that maximizes θ^* .

In the case of equal mortality rates $\mu_f = \mu_m := \mu$, this optimal value is

$$\frac{1}{16} \left(\sqrt{\frac{\mu}{\beta}} + \sqrt{\frac{\mu}{\beta} + 8} \right)^2.$$

Proof. Consider the threshold θ^* written in a more compact form:

$$\theta^* = \frac{\gamma_m}{b} \Big[\sqrt{\gamma_f (\beta - \mu_f + \mu_m)} - \sqrt{\gamma_f \mu_m + \gamma_m \mu_f} \Big]^2.$$

Substituting $\gamma_f := x$ and $\gamma_m := 1 - x$ we can see that maximizing θ^* under the assumption $\mathcal{R}_f > 1$ is equivalent to maximizing the following function in *x* for $\mu_f / \beta \le x \le 1$:

$$h(x) := \frac{1}{b} (1-x) \left[\sqrt{x(\beta - \mu_f + \mu_m)} - \sqrt{x\mu_m + (1-x)\mu_f} \right]^2.$$

It is easy to see that h(1)=0 and also, after some simplifications, that $h(\mu_f/\beta)=0$. This is expected since x = 1 means no male births and $x = \mu_f/\beta$ means there is no net gain in the female reproduction. Since h(x) is positive, continuous and differentiable on $\mu_f/\beta < x < 1$, it will have an absolute maximum $x = x^*$. Its exact value is difficult to obtain in general but it is relatively easy under the assumption of equal mortality rates, $\mu_f = \mu_m := \mu$, while still keeping $\gamma_f \neq \gamma_m$. Setting $R := \beta/\mu > 1$, h(x) becomes

$$h(x) := \frac{1}{R}(1-x)(\sqrt{Rx}-1)^2, \quad \frac{1}{R} \le x \le 1.$$

We now show that h(x) has a unique critical value in its domain. Its first derivative is

$$h'(x) = \frac{1}{R} \left(R - \sqrt{\frac{R}{x}} \right) \left(-2x + \frac{\sqrt{x}}{\sqrt{R}} + 1 \right).$$

The expression in the second set of parentheses can be viewed as a quadratic in \sqrt{x} . We make the change of variable $y := \sqrt{x}$ with $1/\sqrt{R} \le y \le 1$ and the expression becomes

$$k(y) = -2y^2 + \frac{y}{\sqrt{R}} + 1.$$

Notice that k(y) has two real roots, one positive and one negative. The positive root is

$$y^* = \frac{1}{4} \left(\sqrt{\frac{1}{R}} + \sqrt{\frac{1}{R}} + 8 \right).$$

Furthermore

$$k(1) = -1 + \frac{1}{\sqrt{R}} < 0$$
 and $k\left(\frac{1}{\sqrt{R}}\right) = -\frac{1}{R} + 1 > 0$,

since we are under the assumption R > 1. Hence y^* is in the domain $1/\sqrt{R} < y < 1$.

Thus h(x) has a unique critical value

$$x^* = (y^*)^2 = \frac{1}{16} \left(\sqrt{\frac{1}{R}} + \sqrt{\frac{1}{R} + 8} \right)^2.$$

Since h(x) is positive and vanishes at the end points of its domain, it follows that $x = x^*$ maximizes the threshold θ^* .

Remark. Notice that if $R \to \infty$ then $x^* \to \frac{1}{2}$ and if $R \to 1$ then $x^* \to 1$. If we think of *R* as the overall net reproductive number, these limits suggest that if the net-gain rate in the population is unbounded then the optimal sex ratio is even since there will be plenty of individuals of the mate-searching sex (the females) with plenty choices for mating (the males). On the other hand, as the net gain is close to zero, the optimal sex ratio is more and more biased toward the mate-searching sex. These results make intuitive sense and confirm the validity of the optimal female-sex probability at birth as a function of the net reproductive number.

4. Example

We illustrate this result with a numerical example applied to a generic population of mosquitoes. In [Xue et al. 2017] the authors analyze a two-sex population model of mosquitoes deliberately infected by *Wolbachia* bacteria, which is known to reduce the ability of mosquitoes to transmit viral infections such as *Zika* or dengue fever. While the authors do not include Allee effects in their model, they do use different sex probabilities at birth. In [Lounibos and Escher 2008], the authors observed variations in the sex ratio at birth of mosquitoes. We argue here that the inclusion of Allee effects in such models and the computation of the threshold θ^* may be helpful in predicting whether the population of mosquitoes will persist or go extinct.

It is important to point out that persistence happens only if the initial population size is large enough as the Allee effect always causes the extinction equilibrium to be locally asymptotically stable. With larger Allee-effect values, naturally, the

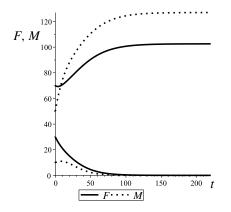


Figure 1. $\theta^* = 81.2$ with suboptimal female-sex probability at birth $\gamma_f = 0.4$. Allee-effect strength used in the example is $\theta = 70$, which leads to population persistence.

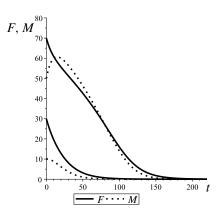


Figure 2. $\theta^* = 81.2$ with suboptimal female-sex probability at birth $\gamma_f = 0.4$. Allee-effect strength used in the example is $\theta = 90$, which leads to extinction.

initial population needs to be larger to escape the basin of attraction of the extinction steady state. Therefore, θ^* indicates a threshold beyond which the Allee effect is strong enough to drive the population to extinction regardless of initial conditions.

In our example below we will use numerical values for the vital parameters from the ranges provided in [Xue et al. 2017] for the mosquito population except θ and the logistic effect *b*. The θ -values are chosen by us to illustrate the result in this section. The logistic effect *b* only affects the overall population size and not the threshold θ^* or any other stability condition. We chose a value for it that provides a clearer figure. In all three figures, these values are $\beta = 0.55$, $\mu_f = 0.05$, $\mu_m = 0.08$ and b = 0.0004.

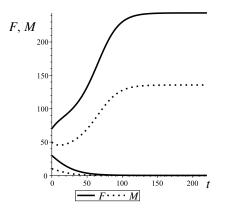


Figure 3. $\theta^* = 108.4$ with optimal female-sex probability at birth $\gamma_f = 0.61$. Allee-effect strength used in the example is $\theta = 90$, which, unlike the suboptimal scenario, now leads to population persistence.

With these values, h(x) becomes

$$h(x) = 2500(1-x)(0.762\sqrt{x} - \sqrt{0.03x + 0.05})^2$$

and, using a computer algebra system, it is straightforward to see that it is maximized, in its domain, for $x^* = 0.61$ and its maximum value is $\theta^* = 108.4$.

First, we use a suboptimal female-sex probability at birth $\gamma_f = 0.4$. Its corresponding threshold is $\theta^* = 81.2$. In Figures 1 and 2 we show an example where the population may persist if $\theta < \theta^*$, while it goes extinct if $\theta > \theta^*$. We chose $\theta = 70$ in the first case and $\theta = 90$ in the second case. Finally, in Figure 3, we use the same Allee effect $\theta = 90$ that caused extinction in the previous case and show that, using the optimal value $\gamma_f = 0.61$, the population now may persist.

5. Conclusions

We analyzed a planar two-sex model with mate-finding Allee effect assuming sex-specific vital parameters: sex ratio at birth and mortality rate. We proved that the total population either goes extinct or exhibits a bistability regimen between a positive steady state and the extinction equilibrium. The specific outcome depends on the strength of the Allee effect. This confirms an earlier result proved under the assumption of equal female and male populations. We further illustrate, with an example, a possible avenue of inquiry which requires maintaining a sex-specific assumption on the model parameters.

There are several limitations of our result that also suggest avenues of future research. First, a planar system for two-sex modeling is not suitable for populations that form long-lasting pairs in order to reproduce. Modeling in this case requires at least three state variables: single females, males and couples. Such behavior is seen in many species and, obviously, is also prevalent in human populations. A next step is then to replicate this analysis for a two-sex model with pair-formation in which F and M will denote the single female and male populations, while a third state variable C will be introduced to model couples. Births will then be a function either exclusively of couples or a mixed system in which births from single individuals are considered as well. The pair-formation term will then contain the mate-finding Allee effect. Since, at the very least, such models will have three equations, the stability analysis will be considerably more difficult.

Another important generalization is to use a different form for the mate-finding Allee effect, possibly one that allows both sexes to play the "mate-searching" role to a various degree. Finally, a generalization that does not even assume a specific Allee-effect form might be desirable since there are already various forms proposed in the literature and a model containing an unspecified one might have a unifying value for this concept. We plan to address some of these questions in the near future.

Acknowledgment

This research was partially supported by NSF Grant DMS-1559912.

References

- [Berec et al. 2018] L. Berec, V. Bernhauerová, and B. Boldin, "Evolution of mate-finding Allee effect in prey", *J. Theoret. Biol.* 441 (2018), 9–18. MR Zbl
- [Courchamp et al. 2008] F. Courchamp, L. Berec, and J. Gascoigne, *Allee effects in ecology and conservation*, Oxford Univ. Press, 2008.
- [Lounibos and Escher 2008] L. P. Lounibos and R. L. Escher, "Sex ratios of mosquitoes from long-term censuses of Florida tree holes", *J. Amer. Mosquito Control Assoc.* 24:1 (2008), 11–15.
- [Mondard et al. 1997] A.-M. Mondard, P. Duncan, H. Fritz, and C. Feh, "Variations in the birth sex ratio and neonatal mortality in a natural herd of horses", *Behav. Ecol. Sociobiol.* **41**:4 (1997), 243–249.
- [Perko 1991] L. Perko, *Differential equations and dynamical systems*, Texts in Appl. Math. **7**, Springer, 1991. MR Zbl
- [Weimerskirch et al. 2005] H. Weimerskirch, J. Lallemand, and J. Martin, "Population sex ratio variation in a monogamous long-lived bird, the wandering albatross", *J. Animal Ecol.* **74**:2 (2005), 285–291.
- [Xue et al. 2017] L. Xue, C. A. Manore, P. Thongsripong, and J. M. Hyman, "Two-sex mosquito model for the persistence of *Wolbachia*", *J. Biol. Dyn.* **11**:suppl. 1 (2017), 216–237. MR

Received: 2019-02-01	Revised: 2019-07-07 Accepted: 2019-07-07
eander35@villanova.edu	Department of Mathematics and Statistics, Villanova University, Villanova, PA, United States
daniel.maxin@valpo.edu	Department of Mathematics and Statistics, Valparaiso University, Valparaiso, IN, United States
jared.ott@huskers.unl.edu	Department of Mathematics, University of Nebraska, Lincoln, NE, United States
gwyneth.terrett@gmail.co	m Mathematics Department, Taylor University, Upland, IN, United States





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Involve (ISSN 1944-4184 electronic, 1944-4176 printed) at Mathematical Sciences Publishers, 798 Evans Hall #3840, c/o University of California, Berkeley, CA 94720-3840, is published continuously online. Periodical rate postage paid at Berkeley, CA 94704, and additional mailing offices.

Involve peer review and production are managed by EditFLOW® from Mathematical Sciences Publishers.

PUBLISHED BY

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