

Evolutionary Dynamics and Strong Allee Effects

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Abstract: We describe the dynamics of an evolutionary model for a population subject to a strong Allee effect. The model assumes the carrying capacity $k(u)$, inherent growth rate $r(u)$, and Allee threshold $a(u)$ are functions of a mean phenotypic trait u subject to evolution. The model is a plane autonomous system that describes the coupled population and mean trait dynamics. We show bounded orbits equilibrate and that the Allee basin shrinks (and can even disappear) as a result of evolution. We also show that stable non-extinction equilibria occur at the local maxima of $k(u)$ and that stable extinction equilibria occur at local minima of $r(u)$. We give examples that illustrate these results and demonstrate other consequences of an Allee threshold in an evolutionary setting. These include the existence of multiple evolutionarily stable, non-extinction equilibria and the possibility of evolving to a non-ESS trait from an initial trait near an ESS.

Keywords: Population dynamics, Allee effects, evolution, evolutionary game theory, ESS

1 Introduction

Population dynamic models are often described by a differential equation of the form $x' = g(x)x$ where $x = x(t)$ is a measure of total population size or density as a function of time t and where $g(x)$ is the per unit growth rate. In devising a model, one requires that $g(x)$ have mathematical properties that incorporate biological and ecological phenomena of interest. Basic phenomena of interest include the stability or instability of the equilibrium $x = 0$ (which addresses the fundamental question of extinction or persistence of a population), bounded or unbounded solutions (which concerns regulated versus unregulated population growth), and the existence and stability of a positive equilibrium state (which concerns the possible equilibration of the population at a “carrying capacity”).

With regard to the extinction-versus-persistence question, the linearization principle implies that extinction can occur (for at least low density populations) if $g(0) < 0$ while it is impossible to occur if $g(0) > 0$. A stable positive equilibrium $x = k > 0$ exists if $g(k) = 0$ and $g'(k) < 0$, that is to say, if there is a positive density k at which per unit growth is 0 and at which there is a negative feedback effect due to increased population density. Indeed, as a mechanism of self-regulated population growth, negative feedback (in the form of deleterious effects on per unit growth due to increased density) is frequently assumed to occur for (at least) large densities, i.e., that $g'(x) < 0$ for (at least) large $x > 0$. Negative feedback at high densities is generally what is meant in ecology by density dependence or regulation.

While it is widely accepted that negative feedback density effects occur at high population densities, it also has long been recognized that positive feedback effects can occur at low population densities, for a variety of biological reasons. Such positive feedback effects are called Allee effects,

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after W. C. Allee who popularized them in numerous writings during the last century (see, for example, the books [2], [3], [4]). By positive feedback is meant that (per unit) growth is enhanced by increased population density, i.e. that $g(x)$ increases with increased (low) density. An Allee effect is present in a model if $g'(x) > 0$ for $x \gtrsim 0$ or, more simply, if $g'(0) > 0$.

There are, of course, infinitely many functional forms for $g(x)$ that can be used to build a differential equation model that incorporates some or all of these fundamental phenomena. Moreover, one might wish to focus on any number of other biological mechanisms involving life history and behavioral traits, environmental factors, and so on, in order to provide biological underpinnings to the mathematical expression for $g(x)$. On the other hand, if one wishes to focus on the basic phenomena described above, in a generic way uncomplicated by other factors, so as to derive simple prototypical models for these phenomena, with a particular interest in extinction, persistence, and Allee effects, then it is natural to consider $g(x)$ for x near 0 and write

$$g(x) = g(0) + g'(0)x + \frac{1}{2}g''(0)x^2 + O(x^3).$$

For example, a moment's reflection shows that the "simplest" (i.e. lowest order) possibility for a model that disallows extinction and possesses regulated growth and equilibration is the linear model $g(x) = g(0) + g'(0)x$ with $g(0) > 0$ and $g'(0) < 0$. The resulting differential equation is, of course, the well-known logistic equation

$$x' = r \left(1 - \frac{x}{k}\right) x, \quad r = g(0) > 0, \quad k = -\frac{r}{g'(0)} > 0$$

which is famously the prototypical model of persistent ($g(0) > 0$) regulated population growth through negative feedback density effects ($g'(0) < 0$).

As a second example, consider Allee effects at low population density, i.e., the case when $g'(0) > 0$. The simplest (lowest order) model with an Allee effect which also has high density regulated (negative feedback) growth is the quadratic model

$$g(x) = g(0) + g'(0)x + \frac{1}{2}g''(0)x^2 \tag{1}$$

with $g''(0) < 0$. If in addition $g(0) > 0$, then the extinction state $x = 0$ is repelling and all populations tend to a unique, stable positive equilibrium $x = k$ (the unique positive root of (1)). The resulting differential equation has the form

$$x' = r \left(1 - \frac{x}{k}\right) \left(1 - \frac{x}{a}\right) x, \quad r = g(0) > 0$$

where $a < 0 < k$ are the roots of the quadratic $g(x)$. This Allee model produces a dynamic similar to the logistic equation in that $x = k$ is a global attractor. If on the other hand $g(0) < 0$, then the extinction state $x = 0$ is stable. Two cases arise depending on whether or not the quadratic (1) has a positive root. If $g(x)$ has no positive roots then $g(x) < 0$ for all $x > 0$ and all populations go extinct. This case occurs if $g'(0)$ is small, specifically, if $g'(0) < (g(0)g''(0)/2)^{1/2}$. If $g(x)$ does have a positive root, then it will necessarily have two positive roots $0 < a < k$. The equilibrium k is stable and the equilibrium a is unstable. This case occurs if the Allee effect is sufficiently strong in the sense that $g'(0) > (g(0)g''(0)/2)^{1/2}$. The resulting differential equation has the form

$$x' = r \left(1 - \frac{x}{k}\right) \left(\frac{x}{a} - 1\right) x \tag{2}$$

where $-r < 0$ is the inherent (low density) per unit growth rate (in this case, decay rate), the positive equilibrium k is the carrying capacity, and the positive equilibrium a is the so-called Allee threshold. Initial population sizes $x(0) > 0$ less than a tend to 0 while initial populations $x(0) > a$ tend to k .

There is a large and growing literature on modeling Allee effects in population dynamics and related fields (e.g., multi-species interactions in ecological systems, disease dynamics and the spread of epidemics, control and management of renewable resource). See [5], [6], [7], [8], [9], [10], [11], [16], [17], [19]. One result of this heightened interest is an ongoing classification of different types of Allee effects and mechanisms. For a recent treatment of Allee effects see [7]. One fundamental distinction made is between weak and strong Allee effects. An Allee effect is called *strong* if it results in the stability of extinction equilibrium $x = 0$ in a model with a stable positive equilibrium. This bistability is the defining hallmark of a strong Allee effect and is a property that is often of central interest in studies of Allee effects.

The differential equation (2) is one prototypical model for a strong Allee effect [7], [12], [17]. We derived the equation (2) by focusing on the properties required of the lowest order terms in $g(x)$ near the extinction equilibrium $x = 0$. Other models $x' = g(x)x$ that describe strong (or weak) Allee effects are certainly possible and derivable based on other criteria and goals. Such models might derive, for example, from sub-models for specific life history traits, behavioral or physiological characteristics, or environmental factors that effect per unit growth. Or one might be interested in a prototypical model that allows for both weak and strong Allee effects, subject to parameter values. For a list of Allee models that have appeared in the literature see [7].

Our goal in this paper is to consider strong Allee effects in the presence of Darwinian evolution. We will use the prototypical model (2) as our starting point and apply to it the methodology of evolutionary game theory. This methodology is the same as that used for the logistic equation in [15], [18]. A model for the evolutionary dynamics of a logistically growing population is

$$\begin{aligned} u' &= \sigma^2 \frac{\partial G(u, x)}{\partial u} \\ x' &= xG(u, x) \end{aligned} \tag{3}$$

$$G(u, x) \doteq r(u) \left(1 - \frac{x}{k(u)} \right).$$

The inherent population growth rate $r > 0$ and the carrying capacity $k > 0$ are assumed dependent on the mean u of a phenotypic trait of the individuals in the population which is subject to Darwinian evolution. The fitness function $G(u, x)$ is therefore a function of both population density x and the mean trait u . The coefficient $\sigma^2 \geq 0$ is the (assumed constant) variance of the trait and is a measure of the speed of evolution. R. Rael studied the global asymptotic dynamics of this plane autonomous system in [14] and showed that all orbits (up to measure 0) with $x(0) > 0$ tend to an equilibrium $(u, x) = (u^*, k(u^*))$ where u^* is a point at which $k(u)$ has a local maximum and, as a result, no population evolves to extinction. (Some technical conditions are needed on k and r at the boundary of the trait interval [14].)

We consider the evolutionary version of the strong Allee model (2)

$$u' = \sigma^2 \frac{\partial G(u, x)}{\partial u} \quad (4a)$$

$$x' = xG(u, x) \quad (4b)$$

$$G(u, x) \doteq r(u) \left(1 - \frac{x}{k(u)}\right) \left(\frac{x}{a(u)} - 1\right). \quad (4c)$$

In this model, the Allee threshold a is also assumed dependent on the mean trait u . The per capita growth rate G given in (4c) is the measure of fitness and, for future reference, we note that

$$\begin{aligned} \frac{\partial G(u, x)}{\partial u} &= r'(u) \left(1 - \frac{x}{k(u)}\right) \left(\frac{x}{a(u)} - 1\right) + r(u) \left(\frac{k'(u)}{k^2(u)} x\right) \left(\frac{x}{a(u)} - 1\right) \\ &\quad + r(u) \left(1 - \frac{x}{k(u)}\right) \left(-\frac{a'(u)}{a^2(u)} x\right). \end{aligned} \quad (5)$$

Our goal is to study the dynamics of the plane autonomous system (4) with an eye towards determining the effect that evolutionary adaptation has on the extinction basin associated with the strong Allee effect. We are interested in ways in which evolutionary change, as described by the properties of the dependencies of r , k and a on the trait u , might enhance or detract from the persistence of the population.

In Section 2 we show, under general conditions, that the Allee basin in the presence of evolution ($\sigma^2 > 0$) is smaller than in the absence of evolution ($\sigma^2 = 0$) and, in this sense, evolution enhances population survival. In Sections 3 and 4 we determine the global asymptotic dynamics of (4). Examples illustrating these results appear in Section 5.

2 The Extinction Basin

Let R denote the real numbers and let R_+ and \bar{R}_+ denote the positive and nonnegative real numbers respectively. Throughout the paper we make the following assumptions about the model coefficients r , k and a in the evolutionary Allee model (4):

A1: $r, k, a \in C^1(U, R_+)$, where $U \doteq \{u : u_1 < u < u_2\}$, $-\infty \leq u_1 < u_2 \leq +\infty$ is an open interval in R and $a(u) < k(u)$ for all $u \in U$.

Initial value problems for the plane autonomous system (4) are well-posed on $U \times R$. Due to the factor of x on the right side of equation (4b), the u -axis in the (u, x) -phase plane is invariant under the flow defined by (4). We say that an initial point $(u(0), x(0)) \in U \times R_+$ is an *extinction point* if the omega limit set of the associated orbit lies on the u -axis. Let $E(\sigma^2)$ denote the set of extinction points, which we refer to as the *extinction basin* of (4). The line segment

$$U^* = \{(u, x) : u \in U, x = 0\}$$

on the u -axis lies in the extinction basin $E(\sigma^2)$ for all $\sigma^2 \geq 0$. In the absence of evolution ($\sigma^2 = 0$) the extinction basin is

$$E(0) = \{(u, x) : u \in U, 0 \leq x < a(u)\}.$$

That is to say, $E(0)$ is the region in the (u, x) -phase plane lying under the *Allee curve* $x = a(u)$.

Assume $\sigma^2 > 0$. At a point lying on the Allee curve $x = a(u)$ we see from (5) that the vector field of (4) has components

$$\begin{aligned} u' &= \sigma^2 r(u) \left(1 - \frac{a(u)}{k(u)} \right) \left(-\frac{a'(u)}{a(u)} \right) \\ x' &= 0. \end{aligned}$$

If $a'(u) = 0$ then the point $(u, a(u))$ is an *Allee equilibrium*. If $a'(u) \neq 0$ then the sign of u' is the sign of $-a'(u)$. This means that in the (u, x) -phase plane the vector field defined by (4) points, from all non-equilibrium points on the Allee curve points, to the right when $a(u)$ is decreasing and to the left when $a(u)$ is increasing. In other words, except at the Allee equilibria, the vector field points *out* of the basin $E(0)$, as shown in Figure 1. As a result orbits near the Allee boundary cross the boundary transversely from the inside to the outside of $E(0)$. It follows that no point outside of $E(0)$ is an extinction point (since U^* is contained in $E(0)$). From this simple observation we have the following result.

Theorem 1 *Assume A1. For $\sigma^2 > 0$ the basin of extinction of $E(\sigma^2)$ is a proper subset of $E(0)$ and $E(0) \setminus E(\sigma^2)$ has positive measure.*

We can interpret this theorem to mean that evolutionary adaptation, as modeled by (4), is advantageous in the sense that it shrinks the Allee basin of extinction. A population with initial point $(u(0), x(0)) \in E(0) \setminus E(\sigma^2)$ for $\sigma^2 > 0$ does not go extinct, although it would go extinct in the absence of evolution ($\sigma^2 = 0$).

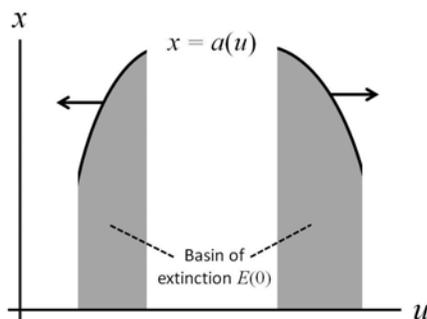


FIGURE 1. When $\sigma^2 = 0$ the extinction base $E(0)$ is the (shaded) region in the (u, x) -plane lying below the Allee curve $x = a(u)$. Increasing and decreasing segments of this curve are displayed. When $\sigma^2 > 0$ the flow field for (4), at points on the boundary $x = a(u)$, points outward from $E(0)$.

3 Equilibria and Local Stability

Assuming evolution occurs, i.e., assuming $\sigma^2 > 0$, the equilibrium equations of the evolutionary Allee model (4) are

$$0 = \frac{\partial G(u, x)}{\partial u} \quad (6a)$$

$$0 = xG(u, x). \quad (6b)$$

From the second equilibrium equation (6b) we see that there are three possibilities for the x component x_e of any equilibrium $(u_e, x_e) \in U \times R$, namely, $x_e = 0$ or $x_e = a(u_e)$ or $x_e = k(u_e)$. To determine the u component for each possibility, we substitute each case into the first equilibrium equation (6a). The following equilibrium alternatives result from an investigation of (5):

$$\begin{aligned} (u_r, 0), u_r \in U, & \text{ is an equilibrium if and only if } r'(u_r) = 0 \\ (u_a, a(u_a)), u_a \in U, & \text{ is an equilibrium if and only if } a'(u_a) = 0 \\ (u_k, k(u_k)), u_k \in U, & \text{ is an equilibrium if and only if } k'(u_k) = 0. \end{aligned} \quad (7)$$

An *extinction equilibrium* (i.e., an equilibrium whose x component equals 0) exists at and only at a trait u_r which is a critical point of the inherent growth rate $r(u)$. Similarly, an *Allee equilibrium* (i.e., an equilibrium whose x component equals a) and a *carrying capacity equilibrium* (i.e., an equilibrium whose x component equals k) exists at and only at mean trait values that are critical points of $a(u)$ and $k(u)$ respectively.

To study the local stability of the equilibria in $U \times \bar{R}_+$ we consider Jacobian of (4)

$$J(u, x) = \begin{pmatrix} \sigma^2 \frac{\partial^2 G(u, x)}{\partial u^2} & \sigma^2 \frac{\partial^2 G(u, x)}{\partial x \partial u} \\ x \frac{\partial G(u, x)}{\partial u} & G(u, x) + x \frac{\partial G(u, x)}{\partial x} \end{pmatrix}. \quad (8)$$

We assume

A2. The critical points of $r(u)$, $a(u)$ and $k(u)$ in U are isolated and the second derivatives $r''(u)$, $a''(u)$ and $k''(u)$ are nonzero at each critical point.

From the equilibrium equation (6a) we see that the lower left entry of $J(u, x)$ equals 0 when evaluated at an equilibrium and, as a result, the eigenvalues of $J(u_e, x_e)$ are the diagonal entries

$$\lambda_1 = \sigma^2 \frac{\partial^2 G(u, x)}{\partial u^2} \Big|_{(u, x) = (u_e, x_e)}, \quad \lambda_2 = G(u_e, x_e) + x \frac{\partial G(u, x)}{\partial x} \Big|_{(u, x) = (u_e, x_e)}.$$

The following table lists the eigenvalues for the three possible equilibrium types (7).

Equilibrium (u, x)	λ_1	λ_2
Extinction: $(u_r, 0)$	$-\sigma^2 r''(u_r)$	$-r(u_r)$
Allee: $(u_a, a(u_a))$	$-\sigma^2 r(u_a) \frac{a''(u_a)}{a(u_a)} \left(1 - \frac{a(u_a)}{k(u_a)}\right)$	$r(u_a) \left(1 - \frac{a(u_a)}{k(u_a)}\right)$
Carrying capacity: $(u_k, k(u_k))$	$\sigma^2 r(u_k) \frac{k''(u_k)}{k(u_k)} \left(\frac{k(u_a)}{a(u_a)} - 1\right)$	$-r(u_k) \left(\frac{k(u_k)}{a(u_k)} - 1\right)$

TABLE 1: The possible equilibria types of the evolutionary Allee model (4) and the eigenvalues of the associated Jacobian $J(u_e, x_e)$.

From the model constraint that $a(u) < k(u)$ for all $u \in U$, we see that $\lambda_1 < 0$ for the extinction and carrying capacity equilibria and $\lambda_1 > 0$ for the Allee equilibrium (which is therefore unstable). The sign of λ_2 depends on the signs second derivatives of r, a and k at the critical trait value, i.e., on the extremal nature of these parameters as functions of the mean trait u . From the Linearization Principle, we obtain the following local stability results.

Theorem 2 *Assume A1 and A2.*

(a) *There exists an extinction equilibrium $(u, x) = (u_r, 0)$ of (4) if and only if u_r is a critical point of $r(u)$. This equilibrium is locally asymptotically stable if $r''(u_r) > 0$ and is a saddle if $r''(u_r) < 0$.*

(b) *There exists an Allee equilibrium $(u, x) = (u_a, a(u_a))$ of (4) if and only if u_a is a critical point of $a(u)$. This equilibrium is always unstable. It is a repeller if $a''(u_a) < 0$ and a saddle if $a''(u_a) > 0$.*

(c) *There exists an carrying capacity equilibrium $(u, x) = (u_k, k(u_k))$ of the evolutionary Allee model (4) if and only if u_k is a critical point of $k(u)$. This equilibrium is locally asymptotically stable if $k''(u_k) < 0$ and is a saddle if $k''(u_k) > 0$.*

Note that the only stable non-extinction equilibria are located at (and only at) the local maxima of the carrying capacity $k(u)$. A necessary condition for a stable equilibrium to be located at an evolutionarily stable strategy (ESS) and, by definition, give rise to an equilibrium that is noninvasive by other species (introduced at low density) is that $\partial^2 G / \partial u^2 \leq 0$ when evaluated at a stable equilibrium [18]. From (5) we find that at any stable non-extinction equilibrium $(u, x) = (u_k, k(u_k))$ meets this necessary condition, since

$$\left. \frac{\partial^2 G(u, x)}{\partial u^2} \right|_{(u, x) = (u_k, k(u_k))} = r(u_k) \frac{k''(u_k)}{k(u_k)} \left(\frac{k(u_k)}{a(u_k)} - 1 \right) < 0,$$

that is to say, since $G(u, k(u_k))$ has a local maximum at $u = u_k$. Sufficient for u_k to be an ESS is that $G(u, k(u_k))$ attain a global maximum on U at $u = u_k$ [18].

4 Global Dynamics

In this section we study the global dynamics of the evolutionary Allee model (4) by means of classic Poincaré-Bendixson theory. Our main goal is to rule out the possibility of cycles and cycle chains of saddles. It then follows from Poincaré-Bendixson theory that all (forward) bounded orbits equilibrate.

As pointed out in Section 2, the u -axis in the (u, x) -phase plane is invariant under the flow defined by the model equations (4), that is to say an initial condition $(u(0), x(0))$ with $x(0) = 0$ implies $x(t) = 0$ for all t . Thus, for all orbits with $x(0) > 0$ we have that $x(t) > 0$ for all t .

The upper half (u, x) -plane is divided into three open, horizontal regions A, B and C by the u -axis and the two curves $x = a(u)$ and $x = k(u)$. See Figure 2. In regions A and C the vector field point downward, since $x' < 0$, while in region B it flows upward. It was shown in Section 2 that the flow on the curve $x = a(u)$ is from A into B. By an similar consideration of (5) on the curve $x = k(u)$ shows that the vector field flows from C into B. These observations rule out the existence of a periodic cycle for (4). A cycle must contain an equilibrium in its interior, all of which lie on the curves $x = k(u)$ and $a = a(u)$ (at their maxima and minima), and a cycle would necessarily have to both enter and leave region C (or region A).

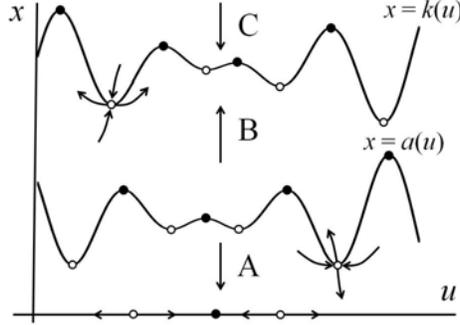


FIGURE 2. Under assumptions A1 and A2 the equilibria of (4a) lie on the maxima and minima of the curves $x = k(u)$ and $x = a(u)$ and on the u -axis located at the maxima and minima of $x = r(u)$. Saddles occur at the minima. Typical saddle structure at the minimum is shown. The flow across $x = k(u)$ is from region C to B and across $x = a(u)$ is from A to B.

Consider the possibility of a cycle chain of heteroclinically connected saddles. According to Theorem 2 saddles occur at the local minima of the curves $x = k(u)$ and $x = a(u)$, in the upper half plane, and on the u -axis at the local minima of $r(u)$. Since the maxima and minima of $r(u)$ alternate along the invariant u -axis, saddles on this axis heteroclinically connect to attractors on this axis (located at the local minima of $r(u)$). It follows that a cycle chain of saddles cannot contain a saddle on the u -axis. Thus, if a cycle chain exists, it must be composed of saddles located at minima of the curves $x = k(u)$ and $x = a(u)$. The local geometric structures of these saddles are shown in Figure 2. A key factor is the horizontal tangency of the unstable and stable manifolds of the saddles on $x = k(u)$ and $x = a(u)$ respectively. This follows from the fact that, at the equilibria on these curves, the lower left entry in the Jacobian (8) equals 0 and the upper left entry is, therefore, an eigenvalue whose eigenvector is the basis vector $\text{col}(1, 0)$. The eigenvalues

$$\sigma^2 \frac{\partial^2 G(u, x)}{\partial u^2} = \begin{cases} \sigma^2 k''(u_k) \frac{r(u_k)}{k(u_k)} \left(\frac{k(u_k)}{a(u_k)} - 1 \right) & \text{for equilibrium } (u_k, k(u_k)) \\ -\sigma^2 \frac{r(u_a)}{a(u_a)} a''(u_a) \left(1 - \frac{a(u_a)}{k(u_a)} \right) & \text{for equilibrium } (u_a, a(u_a)) \end{cases}$$

are positive at saddles located on the curve $x = k(u)$ and negative at saddles located on the curve $x = a(u)$.

The *unstable* manifolds of saddles on the curve $x = k(u)$ are tangentially horizontal and therefore lie in region B. This means they rise (in forward time) in the (u, x) -plane. See Figure 2. For this reason a chain of saddles cannot consist solely of saddles that lie on the curve $x = k(u)$, since each in the chain must be higher in the (u, x) -plane than its predecessor. A similar argument shows that a chain of saddles cannot consist of only saddles on the Allee curve $x = a(u)$, whose *stable* manifolds are tangentially horizontal and therefore lie in region A and decrease (in forward time) in the (u, x) -plane. As a result of these facts, the only possibility for a chain of saddles is for the existence of a heteroclinic connection from a saddle on $x = k(u)$ to a saddle on $x = a(u)$. However, such an orbit would have to cross from region B to A which, as pointed out above, is impossible.

In the absence of cycles and cycle chains, it follows from the Poincaré-Bendixson theory that all bounded orbits remaining in $U \times R_+$ must approach an equilibrium as $t \rightarrow +\infty$. Since the flow in region C is downward, all orbits in the upper half plane ($x(0) \in R_+$) are bounded above. They are, of course, bounded below by the invariant u -axis. However, it is possible, without further assumptions on the model equations, for orbits to approach the boundary of $U \times R_+$, which we denote by $\partial(U \times R_+)$; we give examples in Section 5.1. If U is unbounded, it is possible that orbits are (horizontally) unbounded. In any case, an orbit that remains bounded away from $\partial(U \times R_+)$ is subject to Poincaré-Bendixson theory, and we have the following result.

Theorem 3 *Assume A1 and A2. The evolutionary Allee model (4) has no cycles or cycle chains in $U \times R_+$ and orbits bounded away from $\partial(U \times R_+)$ approach an equilibrium in $U \times \bar{R}_+$.*

Remarks.

(1) Except for stable manifolds of saddles, all orbits in $U \times R_+$ that approach an equilibrium can only approach either a stable, non-extinction equilibrium $(u_k, k(u_k))$ or a stable equilibrium $(u_r, 0)$, in which case the population evolves to extinction.

(2) Modeling assumptions can be made that ensure that orbits remain bounded away from $\partial(U \times R_+)$. For example, in the case of a finite trait interval $U = \{u : u_1 < u < u_2\}$, Rael [14] places constraints on r and k in the evolutionary logistic model (3) so that the flow points into $U \times R_+$ along the vertical boundaries $u = u_1$ and u_2 . Another approach is add terms to the right side of the trait equation (4a) which insure the same thing (such as a positive multiple of $(u - u_1)^2 - (u - u_2)^2$); see [1] for an example. Such conditions are biological motivated by postulating that the boundary traits u_i are extremal traits away from which evolutionary forces move the mean trait, regardless of the population density. In other cases, a biological interpretation can be made of what it means for an orbit to approach the boundary $\partial(U \times R_+)$.

(3) The mean trait interval U is defined, in specific models, as a biologically appropriate interval for the mean phenotypic trait of interest. In some models the coefficients r , k and a might be defined and smooth on a larger open set than U in which case mathematically orbits might cross the vertical portions of the boundary $\partial(U \times R_+)$ located at $u = u_1$ and/or u_2 . There might even exist equilibria on these boundaries which contribute to the relevant phase portrait in $U \times R_+$. Such cases can be analyzed and ecologically interpreted on a case-by-case basis.

5 Examples

In this section we give several examples that illustrate the theory in Sections 3 and 4. The examples in Section 5.1 have a unique non-extinction equilibrium and those in Section 5.2 have several non-extinction equilibria.

5.1 A Unique Non-extinction Equilibrium

Examples 1 and 2 are canonical examples in which there is a single trait at which the population equilibrium level $k(u)$ is maximized and in which trade-offs with both the growth rate $r(u)$ and the Allee threshold $a(u)$; the trait intervals are finite and infinite respectively. In both cases one sees the shrinkage of the Allee basin as predicted by Theorem 1. In Example 3 a trade-off occurs only between $k(u)$ and $a(u)$ and is notable in that the Allee basin totally disappears (up to measure zero) in the presence of evolution. In Example 4, unlike the previous examples, there is not a global correlation between $k(u)$, $a(u)$ and $r(u)$ for all values of the trait u .

Example 1 Suppose the trait interval is defined by finite, extremal trait values $u_1 < u_2$ at which the population carrying capacity $k(u)$ equals 0. Thus, $k(u_i) = 0$ and, by A1, $a(u_i) = 0$ for $i = 1$ and 2. Specifically, in this example we take

$$\begin{aligned} k(u) &= 4k_m u(1-u) \\ a(u) &= 4a_m u(1-u) \\ r(u) &= r_m - u(1-u) \end{aligned} \tag{9}$$

on the trait interval

$$U = \{u : 0 < u < 1\}$$

where $0 < a_m < k_m$. and $r_m > 1/4$. In this model we have assumed trade-offs occur between k , a and r in the sense that $k(u)$ and $a(u)$ have the same monotonicities, but both have the opposite monotonicity of $r(u)$ at each (noncritical) value of u . This means a change in the mean trait u that increases (decreases) the population equilibrium k is accompanied by an increased (decreased) Allee threshold and a decreased (increased) inherent population growth rate r .

In the absence of evolution ($\sigma^2 = 0$) the Allee basin $E(0)$ is the region underneath the parabola $x = a(u)$, shown as the dashed line in Figure 3. Equilibria occur at the maxima of the parabolas $x = k(u)$ and $x = a(u)$ and the minimum of the parabola $x = r(u)$, all of which occur at $u = 1/2$. By Theorem 2 the equilibria $(u_k, k(u_k)) = (1/2, k_m)$ and $(a_r, 0) = (1/2, 0)$ are attractors and $(u_a, a(u_a)) = (1/2, a_m)$ is a repeller.

Near the vertical sides of the boundary $U \times R_+$ located at $u_1 = 0$ and $u_2 = 1$, a straight forward calculation shows

$$\frac{\partial G(u, x)}{\partial u} = \frac{1 - 2u}{16u^3(1-u)^3} F(u, x)$$

where

$$F(u, x) = \begin{cases} \frac{2r_m}{a_m k_m} x^2 + O(u) & \text{for } u \approx 0 \\ \frac{2r_m}{a_m k_m} x^2 + O(1-u) & \text{for } u \approx 1. \end{cases}$$

Thus,

$$\begin{aligned} u' &= \sigma^2 \frac{\partial G(u, x)}{\partial u} > 0 \text{ for } u \gtrsim 0 \text{ and } x > 0 \\ u' &= \sigma^2 \frac{\partial G(u, x)}{\partial u} < 0 \text{ for } u \lesssim 1 \text{ and } x > 0 \end{aligned} \tag{10}$$

and consequently orbits are bounded away from the vertical sides of $\partial(U \times R_+)$ with $x > 0$.

Although we have no general proof, numerical simulations indicate that there exists an orbit that approaches the point $(u, x) = (0, 0)$ lying on $\partial(U \times R_+)$; specifically, there is a heteroclinic orbit that connects the repeller $(u_a, a(u_a)) = (1/4, a_m)$ to the origin. Similarly, there is a heteroclinic orbit that connects this repeller to the point $(u, x) = (1, 0) \in \partial(U \times R_+)$. These are shown as dotted lines in Figure 3. These heteroclinic orbits (together with the saddle point) constitute the boundary of the Allee basin $E(\sigma^2)$, which therefore lies in the interior of the Allee basin $E(0)$ as predicted by Theorem 1. The two cases shown in Figure 3, for two different variances σ^2 , illustrate the dependence of the Allee basin on the speed of evolution. A larger σ^2 (faster evolutionary adaptation) results in a smaller Allee basin.

It is interesting to note in Figure 3 that orbits originating in $E(0)/E(\sigma^2)$ have, before they approach the equilibrium $(u_k, k(u_k)) = (1/2, k_m)$, a transient dynamic along which the mean trait u moves away from $1/2$ and towards an extremal trait ($u = 0$ or 1) and along which the inherent carrying capacity $k(u)$ of the population decreases. Initially the population appears to be in danger of

evolving towards extinction before it (abruptly) recovers and evolves to the non-extinction equilibrium at $(1/2, k_m)$. This reversal occurs because the population, even though it is decreasing, eventually rises above the Allee threshold.

A calculation shows

$$\left. \frac{d^2 G(u, x)}{du^2} \right|_{(u, x) = (1/2, k_m)} = 2(4r_m - 1) \left(1 - \frac{k_m}{a_m} \right) < 0$$

and the necessary condition for $(u, x) = (1/2, k_m)$ to be an ESS is fulfilled. Since there are no other critical points of G (which implies a maximum of G cannot occur at the boundary of U), $G(u, k_m)$ attains a global maximum at $u = 1/2$. This implies the strategy $u = 1/2$ associated with stable equilibrium $(u, x) = (1/2, k_m)$ is an ESS [18].

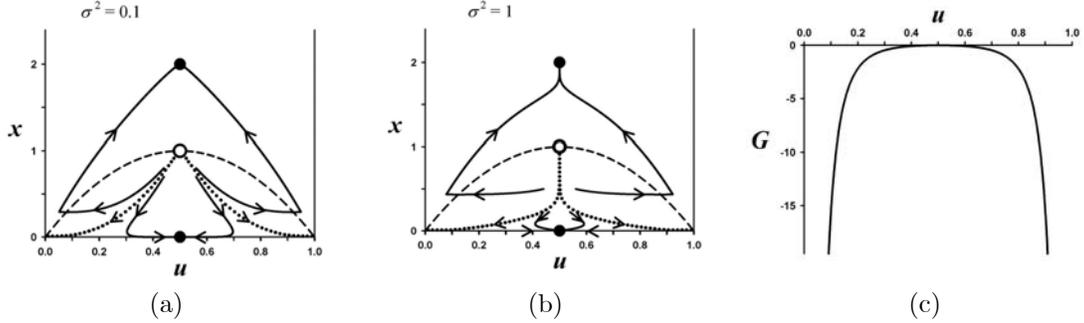


FIGURE 3. (a)-(b) Several orbits are shown in the (u, x) -phase plane associated with the evolutionary Allee model (4) using (9) with $k_m = 2$, $a_m = 1$, $r_m = 2$ and two different variances σ^2 . The dashed line is boundary of the basin of extinction $E(0)$, i.e., the graph of $x = a(u)$, in the absence of evolution ($\sigma^2 = 0$). The dotted lines are orbits that form the boundary of the extinction basin $E(\sigma^2)$ in the presence of evolution ($\sigma^2 > 0$). Two representative orbits are shown whose initial points lie within $E(\sigma^2)$ and two representative orbits are shown whose initial points lie outside $E(\sigma^2)$ but inside $E(0)$. The open circle is a repelling equilibrium and the solid circles are attracting equilibria (Theorem 2). (c) The graph of $G(u, k_m) = G(u, 2)$ shows a global maximum at $u = 1/2$.

The next example shows that a similar phase plane portrait to that in Example 1 but with an infinite trait interval U .

Example 2 Commonly used distributions for model parameters as functions of the mean trait u are Gaussian [18]. For example, a model with trade-off assumptions as in Example 1 is given by the coefficients

$$\begin{aligned} k(u) &= k_m \exp(-u^2/\sigma_k^2) \\ a(u) &= a_m \exp(-u^2/\sigma_a^2) \\ r(u) &= r_m - \exp(-u^2/\sigma_r^2) \end{aligned} \tag{11}$$

defined on the infinite trait interval $U = \mathbb{R}$. In the absence of evolution ($\sigma^2 = 0$) the Allee basin $E(0)$ is the region underneath the bell curve $a(u)$, shown as the dashed line in Figure 3. Equilibria occur at the maxima of $x = k(u)$ and $x = a(u)$ and the minimum of $x = r(u)$, all of which occur at $u = 0$. By Theorem 2 the equilibria $(u_k, k(u_k)) = (0, k_m)$ and $(a_r, 0) = (0, 0)$ are attractors and $(u_a, a(u_a)) = (0, a_m)$ is a repeller. Figure 3 shows two unbounded orbits (dotted lines) that lie beneath the Allee curve $x = a(u)$ and connect the repeller $(0, a_m)$ to the boundary ∂U at $\pm\infty$. These two orbits (together with the saddle) form the boundary of the Allee basin $E(\sigma^2)$ (shown as a dashed line in Figure 3) which is a subset of $E(0)$ as predicted by Theorem 1. As in Example 1 we see that faster evolution (larger σ^2) results in a smaller Allee basin.

A calculation shows

$$\left. \frac{d^2 G(u, x)}{du^2} \right|_{(u, x) = (1/2, k_m)} = \frac{2}{\sigma_k^2} (r_m - 1) \left(1 - \frac{k_m}{a_m} \right) < 0$$

and the necessary condition for $(u, x) = (0, k_m)$ to be an ESS is fulfilled. Since there are no other critical points of G (which implies larger values of G cannot occur as $u \rightarrow \pm\infty$), $G(u, k_m)$ attains a global maximum at $u = 0$. This implies the strategy $u = 0$ associated with the stable equilibrium $(u, x) = (0, k_m)$ is an ESS [18].

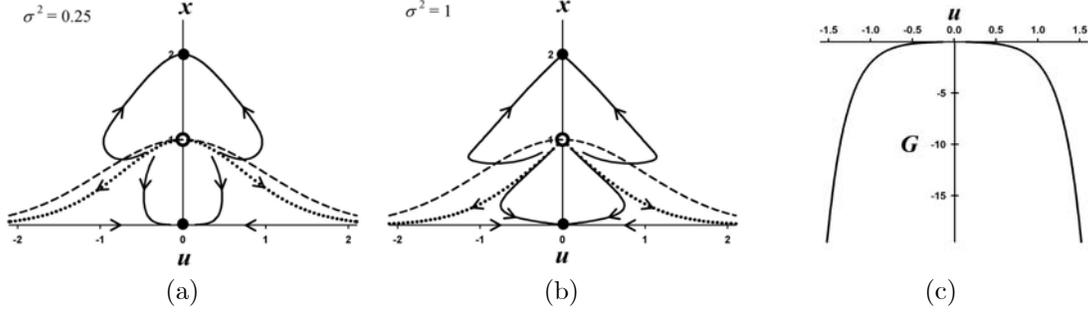


FIGURE 4. (a)-(b) Several orbits are shown in the (u, x) -phase plane associated with the evolutionary Allee model (4) using (11) with $k_m = 2, a_m = 1, r_m = 2, \sigma_k^2 = \sigma_a^2 = \sigma_r^2 = 2$ and two different variances σ^2 . The dashed line is the boundary of the basin of extinction $E(0)$, i.e., the graph of $x = a(u)$, in the absence of evolution ($\sigma^2 = 0$). The dotted lines are orbits that form the boundary of the extinction basin $E(\sigma^2)$ in the presence of evolution ($\sigma^2 > 0$). Two representative orbits are shown whose initial points lie within $E(\sigma^2)$ and two representative orbits are shown whose initial points lie outside $E(\sigma^2)$ but inside $E(0)$. The open circle is a repelling equilibrium and the solid circles are attracting equilibria (Theorem 2). (c) The graph of $G(u, k_m) = G(u, 2)$ shows a global maximum at $u = 0$.

The next example eliminates a trade-off between $k(u)$ and $r(u)$ (while keeping a trade-off between $k(u)$ and $a(u)$). The result is effectively to eliminate the Allee basin altogether.

Example 3 *The coefficients*

$$\begin{aligned} k(u) &= 4k_m u(1-u) \\ a(u) &= 4a_m u(1-u) \\ r(u) &= 4r_m u(1-u) \end{aligned} \tag{12}$$

defined on the trait interval

$$U = \{u : 0 < u < 1\}$$

with $0 < a_m < k_m$ imply a different trade-off scenario from that in Examples 1 and 2. Namely, a change in the mean trait u that increases (decreases) both the population equilibrium k and the inherent growth rate r is accompanied by an increased (decreased) Allee threshold a .

In the absence of evolution ($\sigma^2 = 0$) the Allee basin $E(0)$ is the region underneath the parabola $x = a(u)$, shown as the dashed line in Figure 5. Equilibria occur at the maxima of the parabolas $x = k(u)$, $x = a(u)$ and $x = r(u)$, all of which occur at $u = 1/2$. By Theorem 2 the equilibrium $(u_k, k(u_k)) = (1/2, k_m)$ is an attractor and $(u_a, a(u_a)) = (1/2, a_m)$ is a repeller. Unlike in Examples 1 and 2 the extinction equilibrium $(a_r, 0) = (1/2, 0)$ is now a saddle rather than an attractor.

Near the vertical boundary parts $U \times R_+$ located at $u_1 = 0$ and $u_2 = 1$, a calculation of

$$\frac{dG(u, x)}{du} = \frac{1}{u^2} \frac{1-2u}{(1-u)^2} F(u, x)$$

where

$$F(u, x) = \begin{cases} \frac{r_m}{4a_m k_m} x^2 + O(u^2) & \text{for } u \approx 0 \\ \frac{r_m}{4a_m k_m} x^2 + O((1-u)^2) & \text{for } u \approx 1. \end{cases}$$

This shows (10) holds in this example as well. Thus, as in Example 1, orbits are bounded away from these the vertical sides of $U \times R_+$ for $x > 0$. Unlike in Example 1 and 2, however, no orbits approach the saddle equilibrium $(u_r, 0) = (1/2, 0)$, except for its stable manifold which is a heteroclinic orbit connecting the repeller $(u_a, a(u_a)) = (1/2, a_m)$. Indeed numerical simulations suggest that all orbits, except for this stable manifold, approach the attractor at $(u_k, k(u_k)) = (1/2, k_m)$. Orbits originating within the non-evolutionary basin of attraction $E(0)$ have transients that move towards the extremal trait boundaries at $u = 0$ and $u = 1$ before eventually “turning around” and approaching $(1/2, k_m)$. See Figure 5. Thus, in this example the Allee basin disappears (up to measure 0) in the presence of evolution.

A calculation shows

$$\left. \frac{d^2 G(u, x)}{du^2} \right|_{(u, x) = (1/2, k_m)} = 8r_m \left(1 - \frac{k_m}{a_m} \right) < 0$$

and the necessary condition for $(u, x) = (1/2, k_m)$ to be an ESS is fulfilled. Since there are no other critical points of G (which implies a maximum of G cannot occur at the boundary of U), $G(u, k_m)$ attains a global maximum at $u = 1/2$. This implies the strategy $u = 1/2$ at the stable equilibrium $(u, x) = (1/2, k_m)$ is an ESS [18].

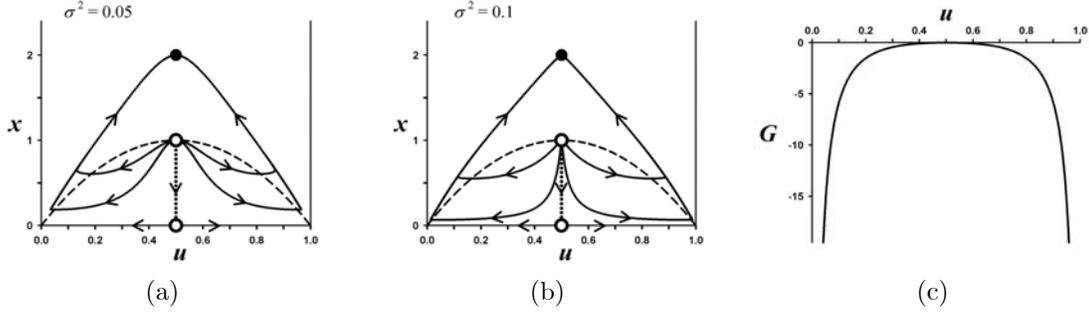


FIGURE 5. (a)-(b) Selected orbits are shown in the (u, x) -phase plane associated with the evolutionary Allee model (4) using (12) with $k_m = 2$, $a_m = 1$, $r_m = 2$ and two different variances σ^2 . The dashed line is the boundary of the extinction basin $E(0)$, i.e., the graph of $x = a(u)$, in the absence of evolution ($\sigma^2 = 0$). With the exception of the vertical orbit (shown as a dotted line) that heteroclinically connects the repeller at $(u_a, a(u_a)) = (1/2, 1)$ to the saddle at $(u_r, 0) = (1/2, 0)$ (shown as open circles), orbits with $x(0) > 0$ tend to the attractor at $(u_k, k(u_k)) = (1/2, 2)$ (shown as a solid circle). (c) The graph of $G(u, k_m) = G(u, 2)$ shows a global maximum at $u = 1/2$.

In the previous examples there are correlated changes in $k(u)$ and $r(u)$ for all values of u . In the final example of this section this correlation is eliminated. One motivation for this assumption can be found in [13], [15].

Example 4 *The coefficient formulas*

$$\begin{aligned}
 k(u) &= 4k_m(u - u^2) \\
 a(u) &= 4a_m(u - u^2) \\
 r(u) &= r_m - \left(u + \frac{1}{4}\right) \left(\frac{3}{4} - u\right) \\
 0 &< a_m < k_m, \quad r_m > \frac{1}{4}
 \end{aligned} \tag{13}$$

differ from those in Example 1 in that the minimum of the growth rate $r(u)$ does not occur at the same trait as the maximum of $k(u)$. Namely, $r(u)$ has a minimum at $u = 1/4$ instead of $1/2$. This means there is not a global trade-off between $k(u)$ and $r(u)$ (i.e., they do not have opposite monotonicity at all traits $u = U = \{0 < u < 1\}$). Nonetheless, Theorems 1, 2, and 3 imply all orbits tend to either the extinction equilibrium $(u, x) = (1/4, 0)$ or the non-extinction equilibrium $(u, x) = (1/2, 2)$ and that the Allee basin shrinks in size in the phase plane. See Figure 6(a). The non-extinction equilibrium is located at an ESS $u = 1/2$ where the G function has a global maximum. See Figure 6(b).

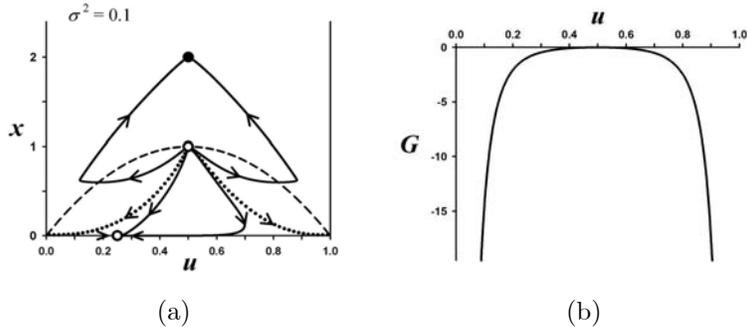


FIGURE 6. (a) Several orbits are shown in the (u, x) -phase plane associated with the evolutionary Allee model (4) using (13) with $k_m = 2$, $a_m = 1$, $r_m = 2$ and $\sigma^2 = 0.1$. The dashed line is boundary of the basin of extinction $E(0)$, i.e., the graph of $x = a(u)$, in the absence of evolution ($\sigma^2 = 0$). The dotted lines are orbits that form the boundary of the extinction basin $E(\sigma^2)$ in the presence of evolution ($\sigma^2 > 0$). Two representative orbits are shown whose initial points lie within $E(\sigma^2)$ and two representative orbits are shown whose initial points lie outside $E(\sigma^2)$ but inside $E(0)$. The open circle is a repelling equilibrium and the solid circles are attracting equilibria (Theorem 2). (b) The graph of $G(u, k_m) = G(u, 2)$ shows a global maximum at $u = 1/2$.

5.2 Multiple Non-extinction Equilibria

If there is more than one trait at which the carrying capacity $k(u)$ has a local maximum, then there is more than one non-extinction equilibrium and the asymptotic state of the evolutionary dynamics will depend on initial conditions. In this section we give examples in which $k(u)$ has two local maxima. An interesting feature of these examples is that there are, due to the influence of the Allee threshold, evolutionary trajectories whose traits take $k(u)$ through the minimum that separates the two maxima of $k(u)$.

We assume $k(u)$ is defined on infinite trait interval $U = R$ and has two local maxima, which we place at $u = \pm 1$, and a local minimum at $u = 0$. We take the Allee basin at each trait, to be a fixed fraction $\varphi < 1$ of $k(u)$, i.e., $a(u) = \varphi k(u)$. This assumes, as in the canonical examples in Section 5.1, a trade-off between $k(u)$ and $a(u)$ in the sense that a change in trait u that increases $k(u)$ is done at the expense of also increasing the Allee threshold. At the trait $u = -1$ we assume (as in Examples 1 and 2) there is a trade-off between $k(u)$ and $r(u)$, i.e. we take $r(u)$ to have a minimum at $u = -1$. We do not assume this trade-off at the trait $u = +1$, however (as in Example 4). See Figure 7.

The formulas used for this example are

$$\begin{aligned}
 k(u) &= k_m \exp\left(-\frac{1}{6}u^6 - \frac{1}{5}bu^5 + \frac{1}{3}bu^3 + \frac{1}{2}u^2\right) \\
 a(u) &= \varphi k(u) \\
 r(u) &= r_m + \rho \left(1 - \exp\left(-\frac{1}{2v}(u+1)^2\right)\right)
 \end{aligned} \tag{14}$$

for $u \in R$ and where the coefficients κ , φ , μ , ρ and v are positive with $\varphi < 1$. For all values of these parameters, the carrying capacity $k(u)$ and Allee threshold $a(u)$ each have two peaks, located at

$u = \pm 1$, separated by a valley at $u = 0$. If b is negative, then the peak at $u = -1$ is the higher peak; if b is positive, then the peak at $u = 1$ is the higher peak. See Figure 7.

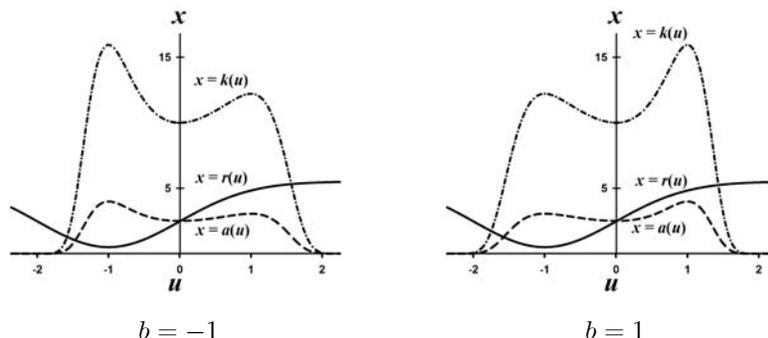


FIGURE 7. Shown are plots of $k(u)$, $a(u)$ and $r(u)$ given by formulas (14) with $k_m = 10$, $\varphi = 1/4$, $r_m = 1/2$, $\rho = 5$, $v = 1$ and $b = \pm 1$.

The results in Sections 3 and 4 imply that all orbits above the Allee boundary tend to one of the two attractors $(u, x) = (-1, x_{-1})$ and $(1, x_1)$ located at the two peaks of $k(u)$ (except for those on the stable manifold of the saddle at the minimum of $k(u)$). Below the Allee boundary, all orbits tend to the extinction attractor located at $u = -1$. The Allee boundary consists of heteroclinic connections running from the repellers at the peaks of $a(u)$ and the saddle at the valley between these two peaks, as well as two unbounded orbits emanating from the peaks which are asymptotic to the u -axis. See the dotted lines in Figures 8(a) and 9(a).

Figures 8(a) and 9(a) show salient features of the phase portraits for the two cases displayed in Figure 7 with $b = -1$ and $b = 1$ respectively. Figures 8(b) and 9(b) show graphs of the fitness functions $G(u, x_{\pm 1})$ associated with the two stable non-extinction equilibria located at the peaks of the carrying capacity $k(u)$. These plots show that the higher peak is associated with an ESS trait, while the lower peak is not. In both cases, some orbits evolve to an ESS and some do not.

Figure 8(a) shows some selected orbits that start near the Allee boundary with traits near $u = -1$ at which the carrying $k(u)$ attains its (global) maximum. As seen in that plot such orbits can asymptotically approach either of the two non-extinction equilibria. Some orbits asymptotically approach the equilibrium located at the ESS trait $u = -1$ where $k(u)$ has its global maximum. Other orbits approach the equilibrium located at the lower peak of $k(u)$ associated with the non-ESS trait $u = +1$. During the time course of the latter orbits, the mean trait u migrates through $u = 0$ at which a minimum of $k(u)$ occurs. Thus, in this case ($b = -1$ in Figure 7), a population can start with a trait near an ESS value (that globally maximizes the carrying capacity) and yet asymptotically evolve to an equilibrium with a non-ESS trait $u = +1$ at a lower carrying capacity (however, with higher growth rate $r(1) > r(-1)$).

When the global maximum occurs at trait $u = 1$ (case $b = 1$ in Figure 7), then this trait is an ESS, as seen in Figure 9. Sample orbits in Figure 9(a) show (as in Figure 8(a)) that orbits starting near the Allee basin with a trait $u = -1$ can either evolve to the non-extinction equilibrium at the lower peak of the carrying capacity k associated with the non-ESS trait $u = -1$ or can evolve to the ESS trait at $u = 1$ where k is globally maximized.

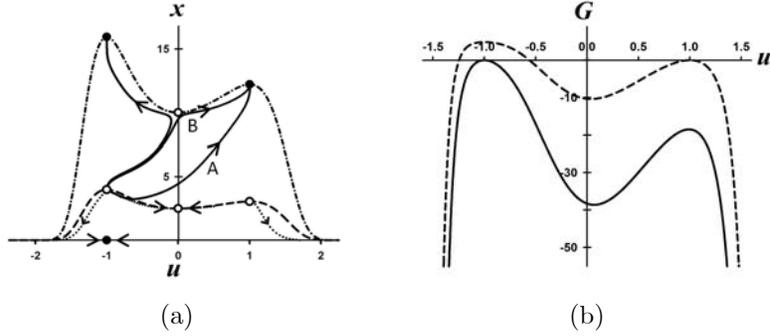


FIGURE 8. (a) Selected orbits are shown in the phase plane portraits of (4) with $k(u)$, $a(u)$ and $r(u)$ given by (14) with parameter values in Figure 7, $b = -1$ and variance is $\sigma^2 = 1$. The dashed line is the graph of $x = a(u)$ and the dash-dot line is the graph of $x = k(u)$. The dotted line is the computed Allee boundary below with orbits asymptotically tend to the equilibrium $(u, x) = (-1, 0)$. The solid circles are equilibrium attractors and the open circles are equilibrium repellers and saddles. The orbits marked A and B are examples of orbits that begin near the Allee boundary with traits near the ESS trait $u = -1$, but which evolve to different equilibria. (b) The G function graphs show that the equilibrium $(u, x) = (-1, x_{-1})$ is an ESS since $G(u, x_{-1})$ attains a global maximum at $u = -1$ (solid line). On the other hand, the equilibrium $(1, x_1) \approx (1, 12214)$ is not an ESS, since $G(u, x_1)$ does not attain a global maximum at $u = +1$ (dashed line).

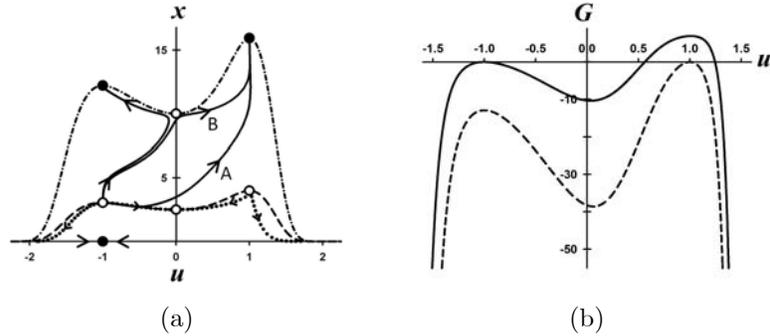


FIGURE 9. These graphs are as in Figure 8 except that $b = 1$ and the higher peak of $k(u)$ occurs at trait $u = 1$. The trait $u = 1$ is an ESS and $u = -1$ is not.

6 Concluding Remarks

The model equations (4) result from the evolutionary logistic model (3) when a strong Allee effect is added to the population's dynamic. In the absence of evolution ($\sigma^2 = 0$) the mean trait u remains unchanged in time and there are two attractors $x = 0$ and $k > 0$ separated by an Allee threshold (repeller) $x = a$. In Sections 3 and 4 we give local and global stability analyses of the plane autonomous system (4) with evolution present ($\sigma^2 > 0$). Our results show that bounded orbits of the evolutionary Allee model (4) asymptotically equilibrate. Specifically, we show that bounded

orbits (to measure zero) tend either to a non-extinction equilibrium $(u, x) = (u_k, k(u_k))$ located at a trait u_k at which the carrying capacity $k(u)$ has a (local) maximum or to an extinction equilibrium $(u, x) = (u_r, 0)$ located at a trait u_r at which the growth rate $k(u)$ has a (local) minimum. This extends the global results of Rael [14] about the evolutionary logistic equation (3) to the case when a strong Allee effect is present. As is to be expected, the presence of a strong Allee effect introduces the possibility that the population will evolve to extinction.

One of our main results is that the Allee basin (the set of orbits that asymptotically approach an extinction equilibrium) in the presence of evolution ($\sigma^2 > 0$) is a proper subset of the Allee basin in the absence of evolution ($\sigma^2 = 0$). Thus, the evolutionary Allee model (4) implies that evolution is beneficial in the sense that reduces the possibility of extinction due to an Allee effect. Indeed, Example 3 in Section 5.1 shows that it is even possible for evolutionary adaptation to eliminate the Allee basin altogether (up to measure 0).

A (locally asymptotically) stable, non-extinction equilibrium (u_e, x_e) , $x_e > 0$, is said to be *evolutionarily stable*. Theorem 2 shows that an evolutionarily stable equilibrium occurs at (and only at) a trait u_e where the carrying capacity $k(u)$ is maximized (at least locally). The trait u_e associated with such an equilibrium is called an ESS if $G(u_e, x_e)$ is a global maximum of $G(u, x_e)$ [18]. At an ESS equilibrium the population is immune to invasion by other species (at low densities). In Section 5.1 we give canonical examples in which the coefficients $k(u)$, $a(u)$, and $r(u)$ have extrema (maxima or minima) at only one trait and incorporate trade-offs with regard to changes in the trait u . In these examples the unique non-extinction equilibrium is an ESS.

The examples in Section 5.2 illustrate evolutionary possibilities when there are more multiple evolutionarily stable, non-extinction equilibrium, i.e., when the carrying capacity $k(u)$ (and Allee threshold) has two or more (local) extrema. In these examples $k(u)$ has two maxima and, as a result, there are two evolutionarily stable, non-extinction equilibria (and one saddle non-extinction equilibrium separating them). The Allee threshold is a fixed fraction of $k(u)$ and these examples model a trade-off between an increased equilibrium level and the threat of an increased Allee threshold. It is shown that an equilibrium trait is an ESS if and only if it is associated with the global maximum of $k(u)$. Thus, when the two local maxima of $k(u)$ are different, it is possible in this model example for populations to evolve to either is a non-extinction equilibrium associated with an ESS trait or one associated with a non-ESS trait, depending on initial conditions.

Orbits in these examples illustrate another interesting possibility due to the presence of an Allee threshold. A population can initially have a trait near an ESS trait and yet asymptotically evolve to a (evolutionarily stable equilibrium) state associated with a non-ESS trait, which requires a transition through a trait at which the carrying capacity has a minimum (at the valley separating its two peaks).

The stability results in Section (3) assume all three parameters r , a and k in the EGT Allee model (4) depend on the mean trait u . Otherwise, equilibria of (4) are not isolated and the linearization principle fails. If, for example, r is independent of u , then every point on the u -axis in the phase plane is an equilibrium. Similarly if a and/or k is independent of u , then every point on the line $x = a$ and/or $x = k$ in the phase plane is an equilibrium. Theorem 1 remains in effect in these cases, but the local and global analysis in Sections (3) and (4) no longer is applicable at these non-hyperbolic equilibria. The mathematical analysis of these cases remains an open problem. Numerical simulations suggest that similar global dynamics hold, however, with the horizontal line of equilibria taking the place of point equilibria as an attractor or repeller. Figure 10 illustrates this assertion by replacing $r(u)$ in Example 2 by a constant r independent of u . A comparison of Figure 10 with Figure 4(a) shows similar phase portraits except that in Figure 10 it is no longer the case

that all orbits in the Allee basin tend asymptotically to the extinction equilibrium at trait $u = 0$. Instead, different orbits in the Allee basin tend asymptotically to different extinction equilibria on the u -axis.

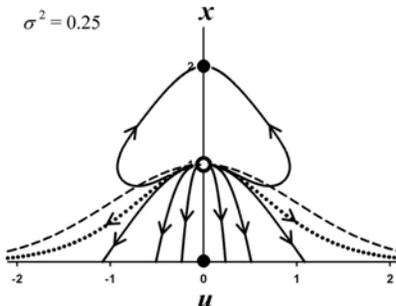


FIGURE 10. Several orbits are shown in the (u, x) -phase plane associated with the evolutionary Allee model (4) using Gaussian $k(u)$ and $a(u)$ as in (11) with $k_m = 2$, $a_m = 1$, and $\sigma_k^2 = \sigma_a^2 = 2$. Unlike in Example 2, however, r does not depend on the trait u and is fixed at $r = 2$. As in Figure 4(a) the dashed line is the boundary of the basin of extinction $E(0)$, i.e., the graph of $x = a(u)$, in the absence of evolution ($\sigma^2 = 0$). The dotted lines are orbits that form the boundary of the extinction basin $E(\sigma^2)$ in the presence of evolution ($\sigma^2 > 0$). All points on the u -axis are equilibria.

Our results in this paper are for one adaptation of the classic logistic equation that includes a strong Allee effect. We suspect that our global analysis of (4) in Sections 2-4, being based on fundamental techniques of linearization and Poincaré-Bendixson theory, can be extended to more general models with strong Allee thresholds.

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