THE EVOLUTIONARY DYNAMICS OF A POPULATION MODEL WITH A STRONG ALLEE EFFECT

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Abstract. An evolutionary game theoretic model for a population subject to predation and a strong Allee threshold of extinction is analyzed using, among other methods, Poincaré-Bendixson theory. The model is a nonlinear, plane autonomous system whose state variables are population density and the mean of a phenotypic trait, which is subject to Darwinian evolution, that determines the population's inherent (low density) growth rate (fitness). A trade-off is assumed in that an increase in the inherent growth rate results in a proportional increase in the predator's attack rate. The main results are that orbits equilibrate (there are no cycles or cycle chains of saddles), that the extinction set (or Allee basin) shrinks when evolution occurs, and that the meant trait component of survival equilibria occur at maxima of the inherent growth rate (as a function of the trait).

1. **Introduction.** There is a growing literature on the modeling and analysis of Allee effects in population dynamics and related fields (e.g., the management of renewable resources and endangered species, ecosystem dynamics, the and the spread of epidemics). See [5, 6, 7, 8, 8, 10, 13, 15, 16, 22, 23, 25]. One result of this interest is an ongoing classification of different types of Allee effects and mechanisms [7]. One basic notion is that of a strong Allee effect, which is a dynamic scenario in which both extinction and survival attractors (usually equilibria) simultaneously exist. This bi-stability is usually considered to be the defining hallmark of an Allee effect and is a property that is often of central interest in studies of Allee effects. The basin of attraction of the extinction state (the Allee basin) is a region in which a population is threatened with extinction. This is the primary motivation for studying models that include mechanisms that result in a strong Allee effect.

Our primary goal in this paper is to study the effect that evolutionary adaptation can have on the Allee basin. Our main ecological result is that this basin shrinks in the presence of evolution, at least for the model considered. By this is meant that there are population states that lead to extinction in the absence of evolution but lead to survival in the presence of evolution (but not vice versa). This is the same general result as obtained in [9], but for a different population model. The differential equation model we consider here is one often used in the study of strong Allee effects [7, 10]. It has more biological underpinnings than the more qualitative

model used in [9] and, unlike the model in [9], can have or not have a strong Allee effect depending on model parameter values. We derive the model in Section 2. It is based on the assumption that model parameters depend on a phenotypic trait that can be subject to Darwinian evolution. We study the model's global dynamics in the absence and in the presence of evolution in Sections 3 and 4 respectively. A specific example in Section 5 illustrates the general results of the global analysis.

2. **Preliminaries.** The phase line portrait of a first order, autonomous differential equation $dx/dt = f(x)$, where $f(x)$ is continuously differentiable on an open interval I of the real line R, consists of equilibria and orbits (of monotone solutions) in I that either approach an equilibrium in I or end point of I (including $+\infty$ and/or $-\infty$). An equilibrium $x = x_e$ is an attractor (respectively a repeller) if $f(x)$ decreases (respectively increases) as x increases through x_e. An equilibrium is, respectively, a right or left shunt if the graph of $f(x)$ has a local minimum or maximum at $x = x_e$. These alternatives can be determined by the geometric properties of the graph of $f(x)$ or analytically, if $f(x)$ is sufficiently differentiable, by derivatives of $f(x)$ evaluated at $x = x_e$.

First order differential equations used to model population dynamics often have the form

$$\frac{dx}{dt} = g(x)x. \tag{1}$$

The per unit growth rate (or population fitness) $g(x)$ is a function of population density x and (because there are no contributions to population growth or decline due to external factors such as immigration or emigration) the equilibrium $x = 0$ represents an extinction state. We suppose $g(x)$ is continuously differentiable on an open interval I containing the nonnegative real numbers $\bar{R}_+$ and that its roots in $\bar{R}_+$ are isolated.

We say that equation (1) has a *strong Allee effect* if there positive initial conditions that lead to extinction and positive initial conditions that do not lead to extinction. Mathematically, equation (1) has a strong Allee effect if there positive initial conditions whose orbits tend to 0 as $t \to +\infty$ and positive initial conditions whose orbits tend to x_k as $t \to +\infty$ where $0 < x_k \leq +\infty$.

A strong Allee effect implies the existence of a positive equilibrium, $x_a > 0$, (a root of $g(x)$) that serves as a threshold between those positive initial conditions (less than x_a) whose orbits approach 0 and those positive initial conditions (greater than x_a) whose orbits do not. The equilibrium x_a is called the *Allee threshold*.

Note that a strong Allee effect implies 0 is either an attractor or a left shunt. Therefore, a necessary condition for a strong Allee effect is $g(0) \leq 0$. Sufficient conditions for a strong Allee effect are $g(0) < 0$ and the existence of a positive root of $g(x)$ (a positive equilibrium).

Most population models assume negative feedback density effects occur for large population densities, which mathematically means $g(x)$ is negative for large values of $x > 0$. This implies orbits with initial conditions larger than x_a are bounded and consequently must approach an equilibrium (larger than or equal to x_a).

The basic prototypical phase line portrait representing a strong Allee effect is $0 \leftarrow x_a \to x_k \leftarrow$ where $x_a > 0$ and $x_k > x_a$ are roots of $g(x)$.

Let v denote the *trait of a typical or focal individual*, let u denote the *population mean of the trait*, and assume that the fitness of an individual depends on its trait v and, possibly, the trait of other individuals as represented by the mean u,

i.e. $g = g(v, u, x)$. A model for the evolutionary or Darwinian dynamics of the population is the plane, autonomous system of differential equations [1, 11, 17, 24]

$$\frac{du}{dt} = \sigma^2 \left. \frac{\partial g(v, u, x)}{\partial v} \right|_{v=u} \tag{2a}$$

$$\frac{dx}{dt} = g(v, u, x) \, x|_{v=u} \tag{2b}$$

Here the parameter $\sigma^2 \geq 0$ in the trait equation (2a), sometimes referred to as Breeder's or Lande's equation, is related to the variation of the phenotypic trait in the population which is assumed constant in time [14, 18, 20].

In the evolutionary model (2) the user must specify an interval $U \subseteq R$ for the mean trait mean trait. The feasible state space for (2) is then $U \times \bar{R}_+$. While it is clear that the x component of an orbit $(u(t), x(t))$ with initial condition in $\bar{R}_+$ remains in $\bar{R}_+$ for all t, it is not in general true that the u component remains in U. The modeler must also place constraints on g so as to keep the u component of orbits within the trait interval U or, alternatively, must decide upon a biological interpretation of what it means should the u component of an orbit leaves U. Note that if $x(0) = 0$ then $x(t) \equiv 0$ for all t (because of the factor of x in the population equation (2b)) and therefore the u-axis in the phase plane is invariant, with a phase line portrait determined by (2a) with $x = 0$. Orbits in the upper half (u, x)-plane must remain in the upper half plane for all t.

In this paper we are interested in the evolutionary model (2) when the population dynamic model (2b) has a strong Allee effect in the absence of evolution. By the absence of evolution we mean when $\sigma^2 = 0$, and hence u remains a fixed constant, and the resulting population dynamic equation (2b) has a strong Allee effect. How does a strong Allee effect affect the evolutionary dynamics when $\sigma^2 > 0$? How does evolutionary adaptation affect the threat of extinction posed by an Allee threshold?

The global dynamics of the evolutionary model (2) were analyzed in ([9]) for the fitness function

$$g(x) \overset{\circ}{=} r \left(1 - \frac{x}{x_k}\right) \left(\frac{x}{x_a} - 1\right) \tag{3}$$
$$r > 0, \quad 0 < x_a < x_k$$

under the assumption that the three model parameters r, x_k and x_a are functions of a phenotypic trait subject to Darwinian evolution. This modification of the classic logistic equation is one generic example of a model with a strong Allee effect [7, 19, 23]. One of the main results from that study was that evolutionary adaptation is beneficial in the sense that the Allee basin (the set of initial conditions whose orbits result in extinction) is a proper subset of the Allee basin in the absence of evolution. Our goal is to do a similar study, with an eye towards addressing this same issue (among others), the model (2) using a different fitness function g possessing a strong Allee effect, one that has often appears in the literature.

Consider a logistically growing population subject to an additional density dependent loss $\delta(x)$:

$$g(x) = r - cx - \delta(x).$$

As in the logistic equation, r is the per capita birth rate a low population density and cx is a per capita death rate due to density effects caused by intraspecific competition. The density dependent loss $\delta(x)$ is due to other causes, such as predation, parasitism, and lost mating opportunities, for example [7].

As pointed out above, necessary for a strong Allee effect in (1) is $r - \delta(0) \leq 0$, and sufficient for a strong Allee effect is $r - \delta(0) < 0$ together with the existence of a positive root of the equation $r - cx - \delta(x) = 0$. In this paper, we will consider the specific case when $\delta(x)$ is a Holling type II function (aka Monod or Michaelis-Menten) [7]

$$\delta(x)\,x = m\frac{x}{\theta + x}, \quad m, \theta > 0.$$

This functional response to increased population density often used to model predation under the assumption that predation saturates with increased prey saturation density. Here m is the maximum predation rate and θ is the half saturation level of predators.

This same functional expression for $\delta(x)$ also arose in a seminal study of Allee effects caused by low density mating limitations [10]. In this paper, we will focus on the predation interpretation and write

$$\delta(x) = a\frac{1}{1 + hax}$$

where $a = m/\theta$ and $h = 1/\theta$ are the predator attack rate and prey handling time respectively [12, 21]. The resulting population dynamic equation

$$\frac{dx}{dt} = (r - cx - a\frac{1}{1 + hax})x. \tag{4}$$

has fitness function

$$g(x) = r - cx - a\frac{1}{1 + hax}. \tag{5}$$

This equation has a strong Allee effect occurs if $r < a$ and the quadratic

$$(a - r) + (c - rha)\,x + chax^2 = 0$$

has a positive root $x > 0$. As a result, the equation (4) has a strong Allee effect for some parameter values, but not for others, which is in contrast to the equation (3) considered in [9].

In this paper we consider the evolutionary model (2) with fitness function (5) under the following assumptions.

(1)   An individual's birth rate $r = r(v)$ is a function of a phenotypic trait v that is subject to evolution.

(2)   The intraspecific competitive effect on the individual's chance of survival is frequency dependent, i.e. depends on how many other individuals have the same trait v which we model by a function of the difference $v - u$. Thus, the competition coefficient $c = c(v - u)$ is a function of the different $v - u$.

(3)   The predator attack rate on individual is a function of the individual's trait v, so that $a = a(v)$.

(4)   The predator attack rate is proportional to the birth rate of prey so that $a(v) = kr(v)$.

We assume the intraspecific competition function $c = c(w)$ satisfies

$$\dot{c}(0) = 0, \quad \ddot{c}(0) < 0$$

where throughout the paper "·" denotes differentiation with respect to a function's argument, e.g.

$$\dot{c}(\delta) \overset{\circ}{=} \frac{dc(w)}{dw}, \quad \ddot{r}(u) \overset{\circ}{=} \frac{d^2r(u)}{du^2}, \quad \text{etc..}$$

The reason we require these two conditions is that we are assuming that the maximum competitive intensity occurs among individuals of the same trait. Consequently, the maximum competitive intensity felt by the individual occurs when its trait v equals the population mean u.

Under the assumptions (1)-(2), the evolutionary equations (2) become

$$\frac{du}{dt} = \sigma^2 \dot{r}(u)\left(1 - \frac{k}{(1 + hkr(u)x)^2}\right) \tag{6a}$$

$$\frac{dx}{dt} = \left(r(u) - cx - \frac{kr(u)}{1 + hkr(u)x}\right)x \tag{6b}$$

where for notational simplicity we denote $c(0)$ by simply $c = c(0)$.

Let

$$U = \{u : u_m < u < u_M\}$$
$$-\infty \leq u_m < u_M \leq +\infty$$

denote the trait interval. We consider the evolutionary equations (6) on the feasible set

$$F \overset{\circ}{=} \bar{U} \times \bar{R}_+.$$

under the smoothness assumption

A1: $r(u) \in C^2\left(\Omega \to R_+^1\right)$ where Ω is an open interval in R such that $\bar{U} \subseteq \Omega$.

With regard to equilibria (u, x) of (6) we distinguish those with $x = 0$, called *extinction equilibria*, and those with $x > 0$, called *survival equilibria*.

Our mathematical goal is to carry out a global analysis of the plane autonomous system (6) on the feasible set F. Specifically, we show that (forward) bounded orbits equilibrate (and, therefore, there are no limit cycles or cycle chains of saddles). We will use the results to address the following questions: which orbits lead to population extinction and which to survival (i.e. which approach an extinction equilibrium and which approach a survival equilibrium)? Is evolutionary adaptation helpful with regard to survival? Specifically, are there orbits that lead to population extinction in the absence of evolution ($\sigma^2 = 0$), but which result in survival when evolution occurs ($\sigma^2 > 0$)? Conversely, are there orbits that lead to survival in the absence of evolution, but which result in extinction when evolution occurs? We will give answers to these questions in Section 4.2.

3. **Non-evolutionary dynamics ($\sigma^2 = 0$).** If $\sigma^2 = 0$ in the system (6), then $du/dt = 0$ and $u \in \bar{U}$ remains fixed in time. All non-equilibrium orbits in $F = \bar{U} \times \bar{R}_+$ are vertical line segments. The population dynamics are governed by the scalar differential equation (6b) for the x component, which we can write as

$$\frac{dx}{dt} = \frac{-p(x, u)}{1 + hkr(u)x}x. \tag{7}$$

where

$$p(x, u) \overset{\circ}{=} (k - 1)r(u) + \left(c - hkr^2(u)\right)x + chkr(u)x^2.$$

Equilibria of (6) in F are the extinction equilibria $(u, 0)$ for any $u \in \bar{U}$ and survival equilibria $(u, x(u))$ for any $u \in \bar{U}$ for which the quadratic polynomial $p(x, u)$ has a positive root $x(u) > 0$.

If $k < 1$ the extinction equilibrium $(u, 0)$ is a repeller (7) and there exists a unique positive attractor at the root

$$x_0(u) = \frac{-\left(c - hkr^2(u)\right) + \sqrt{\left(c - hkr^2(u)\right)^2 - 4chk(k-1)r^2(u)}}{2chkr(u)} \tag{8}$$

of $p(x, u)$, which is a repeller for (7). The (u, x) phase plane portrait for the evolutionary equations (6) in this case is shown in Figure 1(a).

Suppose $k > 1$. Then $p(x, u)$ has no real, positive roots x if $c \geq hkr^2(u)$. If, on the other hand, $c < hkr^2(u)$ then it has two roots

$$x_\pm(u) = \frac{-\left(c - hkr^2(u)\right) \pm \sqrt{\left(c - hkr^2(u)\right)^2 - 4chk(k-1)r^2(u)}}{2chkr(u)} \tag{9}$$

positive provided when u satisfies

$$c < c_0(u)$$

where we have defined

$$c_0(u) \overset{\circ}{=} \left(2k - 1 - 2\sqrt{k(k-1)}\right) hkr^2(u). \tag{10}$$

Note that the parenthetical factor equals 1 at $k = 1$ and monotonically decreases to 0 as $k \to +\infty$. As a result

$$c_0(u) < hkr^2(u) \text{ for } k > 1.$$

We summarize these results in the following theorem.

Theorem 3.1. *Assume A1 and $\sigma^2 = 0$.*

(a) If $k < 1$ then for all values of $u \in \bar{U}$ the evolutionary model (6) has two equilibria in F, namely, the extinction equilibrium $(u, 0)$ and the survival equilibrium $(u, x_0(u))$ where $x_0(u)$ is given by (8).

(b) If $k > 1$ then for each $u \in \bar{U}$, the equilibria (u, x) of the planar system (6) are as follows:

$c_0(u) < c \Rightarrow$ *the extinction equilibria $(u, 0)$ is the only equilibrium;*

$c = c_0(u) \Rightarrow$ *there exist two equilibria, the extinction equilibrium $(u, 0)$ and the survival equilibrium $(u, x_0(u))$ where $x_0(u)$ is given by (8);*

$c_0(u) > c \Rightarrow$ *there exist three equilibria: the extinction equilibrium $(u, 0)$ and two survival equilibria $(u, x_-(u))$ and $(u, x_+(u))$ where $x_-(u) < x_+(u)$ are given by (9).*

The linearization of (7) at the equilibrium $x = 0$ is $dx/dt = r(u)(1-k)x$. When $k < 1$, $x = 0$ is a repeller and when $k > 1$ it is an attractor, giving the phase line portrait

$$\leftarrow 0 \to x(u) \leftarrow$$

When $k > 1$ there are several possible phase line portraits, depending on the value of u :

$$
\begin{array}{ll}
\to 0 \leftarrow & \text{if } c > c_0(u) \\
\to 0 \leftarrow x_0(u) \leftarrow & \text{if } c = c_0(u) \\
\to 0 \leftarrow x_-(u) \to x_+(u) \leftarrow & \text{if } 0 < c < c_0(u)
\end{array}
$$

All these phase plane portrait possibilities are illustrated (vertically) in Figure 1.

When $k < 1$ there are no initial conditions that lead to extinction. When $k > 1$ there are extinction orbits, and we denote *survival and extinction sets* of initial conditions respectively by

$$S_0 \stackrel{\circ}{=} \{(u, x) \in F : c \le c_0(u) \text{ and } x_-(u) \le x\} \tag{11}$$

$$E_0 \stackrel{\circ}{=} F \backslash S_0. \tag{12}$$

The boundary $\partial S_0 = B_1 \cup B_2^L \cup B_2^R \cup B_3$ of the survival region S_0 consists of

(a)   a lower portion B_1 defined by the curve $x = x_-(u)$ between roots $u = u_0$ of $c = c_0(u)$ and at which the two survival equilibria $x_+(u_0) = x_-(u_0)$ coalesce);

(b)   vertical half lines B_2^L and B_2^R located at $u = u_0$ for $x \ge x_0$;   (13)

(c)   vertical line segments B_3 located at a boundary point $u = u_m$ and/or $u = u_M$ (for $x > x_-(u_m)$ and/or $x > x_-(u_M)$).
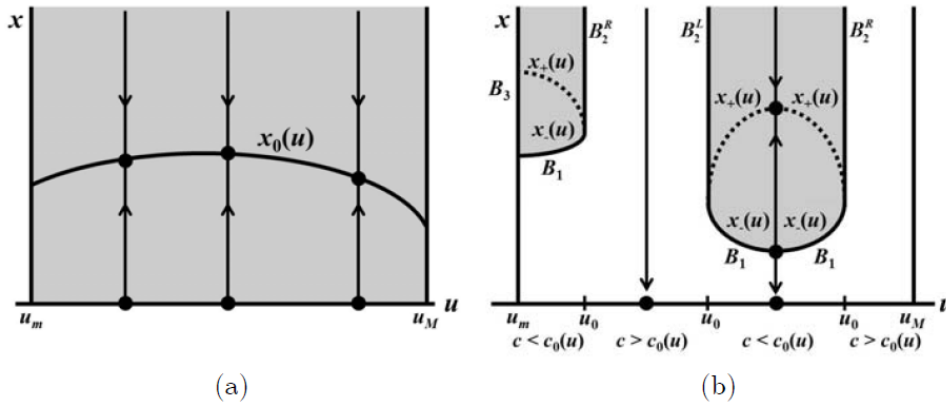
See Figure 1(b).

(a)   (b)

Figure 1. Assume $\sigma^2 = 0$ in (6). The phase plane portrait on F of (6) is shown in the two cases when $k < 1$ and $k > 1$. *All non-equilibrium orbits are vertical line segments* and equilibrate as $t \to +\infty$. The survival set S_0 is the shaded region and the extinction set E_0 is the unshaded region.

(a) When $k < 1$ all orbits approach the survival equilibrium $(u, x_0(u))$ given by (8). Three sample vertical phase line portraits are shown.

(b) When $k > 1$ some orbits approach an extinction equilibrium $(u, 0)$ and some approach a survival equilibrium $(u, x_+(u))$.

4. **Evolutionary dynamics ($\sigma^2 > 0$).** Our goal is to carry out a global analysis of the (u, x)-phase plane of the evolutionary model (6) by means of Poincaré-Bendixson theory. We will also compare the extinction set, i.e. the set of initial conditions in F whose orbits lead to population extinction when $\sigma^2 > 0$, to the extinction set E_0 when $\sigma^2 = 0$. We begin with a study of equilibria and their local stability properties obtained by the linearization principle.

4.1. **Local analysis of equilibria.** The equilibrium equations of (6) are

$$0 = \dot{r}(u)\left(1 - \frac{k}{(1 + hkr(u)x)^2}\right) \tag{14a}$$

$$0 = \left(r(u) - cx - \frac{kr(u)}{1 + hkr(u)x}\right)x \tag{14b}$$

The lower left entry in the Jacobian

$$J(u,x) = \begin{pmatrix} \frac{\partial}{\partial u}\sigma^2\dot{r}(u)\left(1 - \frac{k}{(1+hkr(u)x)^2}\right) & \frac{\partial}{\partial x}\sigma^2\dot{r}(u)\left(1 - \frac{k}{(1+hkr(u)x)^2}\right) \\ \frac{\partial}{\partial u}\left(r(u) - cx - \frac{kr(u)}{1+hkr(u)x}\right)x & \frac{\partial}{\partial x}\left(r(u) - cx - \frac{kr(u)}{1+hkr(u)x}\right)x \end{pmatrix}$$

equals 0 when evaluated at an equilibrium (u,x). This is obvious if $x = 0$ and follows by the trait equilibrium equation (14a) if $x \neq 0$. Thus, the eigenvalues are the diagonal entries evaluated at the equilibrium, namely

$$\lambda_1(u,x) \stackrel{\circ}{=} \sigma^2\ddot{r}(u)\left(1 - \frac{k}{(1 + hkr(u)x)^2}\right)$$
$$+ \sigma^2\dot{r}(u)\left(2\frac{hk^2\dot{r}(u)x}{(1 + hkr(u)x)^3}\right) \tag{15}$$

$$\lambda_2(u,x) \stackrel{\circ}{=} \left(r(u) - cx - \frac{kr(u)}{1 + hkr(u)x}\right)$$
$$+ \left(-c + \frac{hk^2r^2(u)}{(1 + hkr(u)x)^2}\right)x. \tag{16}$$

We first turn our attention to extinction equilibria. We define a *critical trait* to be a real number $u^* \in \Omega$ such that $\dot{r}(u^*) = 0$. From (14) we see that a pair $(u,x) = (u^*, 0) \in F$ is an *extinction equilibrium* if and only if

$$\dot{r}(u^*)(1 - k) = 0$$

If $k = 1$ then $(u^*, 0)$ is an extinction equilibria for all $u^* \in \bar{U}$. Moreover, $\lambda_1(u^*, 0) = 0$ and the equilibrium is nonhyperbolic and the linearization principle fails. We ignore this nongeneric case and assume if $k \neq 1$. In this case $(u^*, 0)$ is an extinction equilibrium if and only if u^* is a critical point of $r(u)$. The eigenvalues eigenvalues of the Jacobian at an extinction equilibrium are

$$\lambda_1(u,0) = \sigma^2\ddot{r}(u^*)(1 - k), \qquad \lambda_2(u^*, 0) = (1 - k)r(u^*).$$

The linearization principle implies the following result.

Theorem 4.1. *Assume A1 and let $u^* \in \bar{U}$ be a critical trait of $r(u)$.*
(a) If $k < 1$ then the extinction equilibrium $(u^*, 0)$ is unstable.
(b) If $k > 1$, we have the following alternatives:
   (i) $\ddot{r}(u^*) > 0$ implies the extinction equilibrium $(u^*, 0)$
      is a locally asymptotically stable (LAS) node;
   (ii) $\ddot{r}(u^*) < 0$ implies the extinction equilibrium $(u^*, 0)$ is a saddle.

Theorem 4.1 gives criteria for the instability and stability of an extinction equilibrium $(u^*, 0)$. If $k < 1$ then any extinction equilibrium is unstable in both the evolutionary and non-evolutionary model. Since our interest is on the interplay of

extinction versus survival and the effect of evolution on the extinction basin, we will focus on the case $k > 1$.

We next turn our attention to survival equilibria. The algebraic equations for survival equilibria (u, x), $x > 0$, are

$$0 = \dot{r}(u)\left(1 - \frac{k}{(1 + hkr(u)x)^2}\right) \tag{17a}$$

$$0 = r(u) - cx - \frac{kr(u)}{1 + hkr(u)x}. \tag{17b}$$

We begin be observing that if (u, x) solves these equations with $x > 0$, then it must be true that $\dot{r}(u) = 0$ (i.e. that u is a critical trait u^*). To see this, suppose $\dot{r}(u) \neq 0$. Then (u, x) solves the equation

$$\frac{k}{(1 + hkr(u)x)^2} = 1$$

which when used in (17b) yields

$$0 = r(u) - cx - (1 + hkr(u)x)r(u)$$

or $\left(c + hkr^2(u)\right)x = 0$, which implies the contradiction $x = 0$. Therefore, the u-component in a survival equilibria (u, x) must be a critical trait. The x-component is a positive root of equation (17b), which is an algebraic equation we studied in the non-evolution case in Section 3.

Theorem 4.2. *Assume A1, $\sigma^2 > 0$ and $k > 1$. The only equilibria of the evolution equations (6) in F are located at critical traits of $r(u)$ in $\bar{U}$. Suppose $u^* \in \bar{U}$ is a critical trait of $r(u)$. In addition to the extinction equilibrium $(u^*, 0)$, there*
   (a) are two survival equilibria $(u^*, x_\pm(u^*))$ if $c < c_0(u^*)$
       where $x_-(u) < x_+(u)$ are given by (9);
   (b) is one survival equilibrium $(u^*, x_0(u^*))$ if $c = c_0(u^*)$;
   (c) are no survival equilibria at $u = u^*$ if $c > c_0(u^*)$.

To obtain stability criteria for a survival equilibrium by means of the linearization principle, we investigate the eigenvalues (15) and (16) of the Jacobian evaluated at the two survival equilibria $(u^*, x_\pm(u^*))$. Our first observation is that the inequalities

$$\lambda_2(u^*, x_-(u^*)) > 0 \quad \text{and} \quad \lambda_2(u^*, x_+(u^*)) < 0 \tag{18}$$

follow from the analysis of the non-evolutionary case. As a result *the equilibrium $(u^*, x_-(u^*))$ is always unstable.* The local stability and phase portrait of $(u, x_\pm(u))$ depends on the signs of the remaining eigenvalues

$$\lambda_1(u^*, x_-(u^*)) \quad \text{and} \quad \lambda_1(u^*, x_+(u^*)).$$

From (17b) follows

$$\frac{r(u^*) - cx}{r(u^*)} = \frac{k}{1 + hkr(u^*)x_\pm(u^*)},$$

from which in turn follow

$$r(u^*) - cx_\pm(u^*) > 0 \tag{19}$$

and

$$
\begin{aligned}
\lambda_1\left(u^*, x_\pm\left(u^*\right)\right) & = \sigma^2 \ddot{r}\left(u^*\right)\left(1 - \frac{k}{\left(1 + h k r\left(u^*\right) x_\pm\left(u^*\right)\right)^2}\right) \\
& = \sigma^2 \ddot{r}\left(u^*\right) \frac{1}{k}\left(\sqrt{k} - 1 + \frac{c x_\pm\left(u^*\right)}{r\left(u^*\right)}\right)\left(\sqrt{k} + \frac{r\left(u^*\right) - c x_\pm\left(u^*\right)}{r\left(u^*\right)}\right).
\end{aligned}
$$

Both parenthetical expressions are positive by (19) and our assumption that $k > 1$. Consequently

$$
\operatorname{sign} \lambda_1\left(u^*, x_\pm\left(u^*\right)\right) = \operatorname{sign} \ddot{r}\left(u^*\right) \tag{20}
$$

From (18), (20) and Theorem 4.1 we get the following result.

Theorem 4.3. *Assume A1, $\sigma^2 > 0$, and $k > 1$. The only equilibria of the evolutionary equations (6) in F are located at critical traits of $r(u)$ in $\bar{U}$. If $u^* \in \bar{U}$ is a critical trait of $r(u)$ then we have the following alternatives.*

(a) Suppose $\ddot{r}(u^*) < 0$. Then

(i) $c > c_0(u^*)$ implies the only equilibrium is $(u^*, 0)$ and it is a saddle.

(ii) $c < c_0(u^*)$ implies there are three equilibria:

$$
\begin{aligned}
(u^*, 0) & \quad \text{a saddle} \\
(u^*, x_-(u^*)) & \quad \text{a saddle} \\
(u^*, x_+(u^*)) & \quad \text{a stable node.}
\end{aligned}
$$

(b) Suppose $\ddot{r}(u^*) > 0$. Then

(i) $c > c_0(u^*)$ implies the only equilibrium is $(u^*, 0)$ and it is a stable node.

(ii) $c < c_0(u^*)$ implies there are three equilibria:

$$
\begin{aligned}
(u^*, 0) & \quad \text{a stable node} \\
(u^*, x_-(u^*)) & \quad \text{an unstable node} \\
(u^*, x_+(u^*)) & \quad \text{a saddle.}
\end{aligned}
$$

Note 1. Stable survival equilibria are located at critical traits at which $r(u)$ (and hence of $a(u)$) has a local *maximum*.

Note 2. Stable survival equilibria occur only when the negative feedback of intraspecific competition, as measured by c, is small enough, i.e. $c < c_0(u^*)$.

Note 3. The case $c = c_0(u^*)$ does not appear in Theorem 4.3. In this case a unique survival equilibrium occurs as the equilibria $x_+(u^*) = x_-(u^*)$ coalesce at $x_0(u^*)$. This equilibrium is nonhyperbolic and linearization fails. The stability criteria of Theorem 4.1 for the extinction equilibrium $(u^*, 0)$ remain valid, however.

4.2. **Global dynamics.** From the evolutionary equations (6) we see that an initial condition (u, x) with $x > 0$ and $u = u^*$, where $u^* \in \bar{U}$ is a critical trait of $r(u)$, produces an orbit $(u^*, x(t))$ with a fixed u-component and where the x component is a solution $x(t)$ of the equation

$$
\frac{dx}{dt} = \left(r\left(u^*\right) - c x - \frac{k r\left(u^*\right)}{1 + h k r\left(u^*\right) x}\right) x.
$$

These orbits are vertical lines in the upper half (u, x)-phase plane. Also, an initial condition (u, x) with $x = 0$ produces an orbit $(u(t), 0)$ where $u(t)$ is a solution of the equation

$$
\frac{du}{dt} = \sigma^2 \dot{r}(u)(1 - k)
$$

These orbits lie along the horizontal u-axis in the (u, x)-phase plane. As a result no orbit can leave the upper half plane.

For $u_1, u_2 \in \bar{U}$, $u_1 < u_2$, define the semi-infinite rectangle

$$F(u_1, u_2) = \{(u, x) : u_1 < u < u_2, \ x > 0\}.$$

From our observations above, we have the following result.

Theorem 4.4. *Let $u_1^* < u_2^*$ be two critical points of $r(u)$ in $\bar{U}$. The semi-infinite rectangular region $F(u_1^*, u_2^*)$, its boundary $\partial F(u_1^*, u_2^*)$ (and therefore its closure $\bar{F}(u_1^*, u_2^*)$) are invariant sets.*

We assume:

A2: $r(u)$ is bounded on $\bar{U}$ and has finite number $n \geq 1$ of critical points $u_1^* < u_2^* < \cdots < u_n^*$ in $\bar{U}$ at which $\ddot{r}(u_i^*) \neq 0$.

We write the feasible state space F as a union of the invariant, semi-infinite rectangles created by the critical points u_i (and the endpoints u_m, u_M)

$$F = F(u_m, u_1^*) \cup_{i=1}^{n-1} \bar{F}(u_i^*, u_{i+1}^*) \cup F(u_n^*, u_M).$$

Equilibrium points in F can only occur on a vertical side of a rectangle located at a critical trait u_i^*. Note that an endpoint u_m and/or u_M is allowed to be a critical trait. Moreover, the vertical sides $\bar{F}(u_i^*, u_{i+1}^*)$ are invariant (they consist of orbits). It follows that *there exist no cycles or cycle chains of saddle* (since either of these must surround an equilibrium) in F. From Poincaré-Bendixson theory we conclude that all (forward) bounded orbits remaining in F must equilibrate as $t \to +\infty$. All orbits in the invariant set $\bar{F}(u_i^*, u_{i+1}^*)$ are indeed forward bounded. This is because the right side of the differential equation (6b) is bounded by $(r_m - cx)x$ and hence is negative when $x > r_m/c$. Thus, the vector field at points $(u, x) \in F(u_i^*, u_{i+1}^*)$ with $x > r_m/c$ points downward in the (u, x)-phase plane. We have arrived at the following results.

Theorem 4.5. *Assume A1 and A2. A forward bounded orbit of the evolution equations (6) that remains in F approaches an equilibrium as $t \to +\infty$. In particular, all orbits in the invariant sets $\bar{F}(u_i^*, u_{i+1}^*)$, $i = 1, 2, \ldots, n-1$, approach, as $t \to +\infty$, an equilibrium (u, x) located on the boundary of $\bar{F}(u_i^*, u_{i+1}^*)$.*

Corollary 1. *Assume A1, A2 and that the endpoints $u_m = u_1$ and $u_M = u_n$ of U are critical traits, i.e. assume that*

$$F = \cup_{i=1}^{n-1} \bar{F}(u_i^*, u_{i+1}^*). \tag{21}$$

Then all orbits of the evolution equations (6) in F approach an equilibrium as $t \to +\infty$.

Note 4. If u_m is not a critical trait, then the global dynamics in the invariant region $F(u_m, u_1^*)$ depends on the dynamics near the boundary at u_m. Orbits in this region might not remain in this region or be forward bounded. For example, if u_m is finite and not a critical point, then an inspection of the sign of the right side of equation trait equation (6a) is the same as the sign of $\dot{r}(u_m)$ when $x >> 0$, but is the opposite of the sign of $\dot{r}(u_m)$ for $x \approx 0$ if $k > 1$. Therefore, along the left vertical boundary of $F(u_m, u_1)$ at $u = u_m$ the vector field points in opposite directions for large and small values of x. This means that not all orbits in $F(u_m, u_1)$ will remain in $F(u_m, u_1)$ as $t \to +\infty$. A similar conclusion holds for orbits in $F(u_n^*, u_M)$ if u_M is finite and not a critical trait. On the other hand, if $u_m = -\infty$ and/or $u_M = +\infty$ then it is a possibility that some orbits will not be forward bounded in their u component. In these cases, the modeler must decide what biological meaning is

to be ascribe to orbits that leave the feasible region F or have unbounded trait components u.

Finally we consider the question of whether or not evolution can change the long term survival of a population whose dynamics are modeled by the equations (6). Specifically, we address two questions:

$$
\begin{array}{ll}
\text{Q1:} & \text{Are there initial points in } F \text{ whose orbits approach an} \\
& \text{extinction equilibrium when evolution occurs } (\sigma^2 > 0) \\
& \text{but approach a survival equilibrium when evolution} \\
& \text{is absent } (\sigma^2 = 0)?
\end{array} \tag{22}
$$

$$
\begin{array}{ll}
\text{Q2:} & \text{Are there initial points in } F \text{ whose orbits approach a} \\
& \text{survival equilibrium when evolution is absent } (\sigma^2 = 0) \\
& \text{but approach an extinction equilibrium when evolution} \\
& \text{occurs } (\sigma^2 > 0)?
\end{array} \tag{23}
$$

To answer these questions, we define the *extinction and survival sets* E_{σ^2} and S_{σ^2} when $\sigma^2 > 0$ to be, respectively, the set of initial conditions whose orbits approach an extinction equilibrium and the set of initial conditions whose orbits approach a survival equilibrium. We want to compare E_{σ^2} and S_{σ^2} when $\sigma^2 > 0$ to the extinction and survival sets E_0 and S_0 when evolution is absent.

We restrict our analysis to the (invariant) subset $\cup_{i=1}^{n-1} \bar{F}\left(u_i^*, u_{i+1}^*\right)$ of the feasible set F, ignoring the end regions $F\left(u_m, u_1^*\right)$ and $F\left(u_n^*, u_M\right)$ on which the global dynamics cannot be determined without further restrictions on the model equations for traits u near the endpoints u_m and u_M of U (see Note 4). Equivalently, we assume u_m and u_M are critical traits and, hence, the feasible set is (21).

First, we note that if $c > c_0(u)$ for all $u \in \bar{U}$, then in the absence of evolution all orbits tend to an extinction equilibrium. When evolution occurs, there exist no survival equilibria in F, in which case all orbits tend to an extinction equilibrium (Corollary 1). Therefore, evolution does not change the asymptotic outcome of extinction in this case, and the answers to both questions Q1 and Q2 is no. Therefore, we assume

A3: $u_m = u_1^*$ and $u_M = u_n^*$ are critical points and there exists a trait
      $u \in F$ for which $c < c_0(u)$.

If A3 holds, then by continuity $c < c_0(u)$ holds on an open set in U and the set S_0 defined by (11) is nonempty and has an open interior. The proof of the following theorem appears in the Appendix.

Theorem 4.6. *Assume A1, A2, and A3 hold and that $\sigma^2 > 0$ and $k > 1$. Then set S_0 is a proper subset of the extinction set S_{σ^2} of (6) and $S_{\sigma^2} \backslash S_0$ has positive measure.*

5. **Example.** We consider an example designed to illustrate the analytic results in Section 4. This example assumes a trait interval that is bounded by two extreme mean trait values u_m and u_M at which the population inherent growth rate rapidly drops to 0, that is to say, at which $r(u)$ and $\dot{r}(u)$ vanish. Obviously, $r(u)$ attains a maximum somewhere in the interval U. We assume that $r(u)$ attains its maximum at a trait value u_c where $\ddot{r}(u)$ is negative and that there exists no other other critical points in U. In such a case, there are three extinction equilibria, one located at each of the traits $u = u_m$, u_c and u_M. Theorem 4.5 gives conditions under which all orbits equilibrate.

By Theorems [4.1] and [4.3] the extinction equilibria $(u, x) = (u_m, 0)$ and $(u_M, 0)$ are stable nodes and $(u_c, 0)$ is a saddle. If $c > c_0(u_c)$ all orbits (except for the stable manifold of $(u_c, 0)$) tend to an extinction equilibrium, specifically to either $(u, x) = (u_m, 0)$ or $(u_M, 0)$. If $c < c_0(u_c)$ then there exist two survival equilibria at $u = u_c$, namely a saddle at $(u, x) = (u_c, u_-(u_c))$ and a stable node at $(u_c, x_+(u_c))$. In this case, the survival equilibrium $(u, x) = (u_c, x_-(u_c))$ and its stable manifold constitute the boundary between the extinction and survival sets E_{σ^2} and S_{σ^2}.

Figure 2 illustrates these dynamics, as well as the shrinkage of the extinction set E_{σ^2} implied by Theorem [4.6], using the specific example

$$r(v) = 16mv^2(1-v)^2 \quad \text{on trait interval } 0 \le v \le 1 \text{ with } m > 0. \qquad (24)$$

For this example, $u_m = 0$ and $u_M = 1$ and $r(u)$ attains a maximum of m at $u_c = 1/2$. From [(10)] we have

$$c_0(1/2) = \left(2k - 1 - 2\sqrt{k(k-1)}\right)hkm^2.$$

For $c < c_0(1/2)$ there exist two survival equilibria (u, x) which are given by the formulas

$$(1/2, x_+(1/2)) = \left(\frac{1}{2}, \frac{hkm^2 - c + \sqrt{(hkm^2 - c)^2 - 4chkm^2(k-1)}}{2chkm}\right)$$

$$(1/2, x_-(1/2)) = \left(\frac{1}{2}, \frac{hkm^2 - c - \sqrt{(hkm^2 - c)^2 - 4chkm^2(k-1)}}{2chkm}\right).$$

All orbits in $U \times R_+$, other than the stable manifolds of the saddle $(1/2, x_-(1/2))$, approach either an extinction equilibrium $(u, x) = (0, 0)$ or $(1, 0)$ or the survival equilibrium $(u, x) = (1/2, x_+(1/2))$. Some sample orbits are shown in Figure 2.

For $c > c_0(1/2)$ there are no survival equilibria and all orbits tend to an extinction equilibrium. See Figure 2a.

For $c < c_0(1/2)$ there exist survival equilibria $(1/2, x_\pm(1/2))$, as shown in Figure 2b. The stable manifold of $(u, x) = (1/2, x_-(1/2))$ is the boundary of the extinction set, which lies below it. The vertical line segments B_2^L and B_2^R lie above the stable manifold and consequently the survival set has expanded in the presence of evolution (compare to the survival set in Figure 1b). To illustrate this point, three orbits that would lie in the extinction set E_0 in the absence of evolution are shown in Figure 2b, two of which.

This example illustrates several ecological and evolutionary possibilities. First, if the intensity of intraspecific competition is sufficiently high ($c > c_0(1/2)$), the population will be driven to extinction. The evolutionary trajectory drives the phenotypic trait to a value ($v = 0$ or 1) where the population growth rate $r(v)$ vanishes. Although along most orbits in Figure 2a there is an initial trend towards trait $v = 1/2$ where the growth rate is maximized, this evolutionary trend is not sufficient to save the population from extinction.

On the other hand, if the intensity of intraspecific competition is sufficiently weak ($c < c_0(1/2)$), then the evolutionary trajectories occur that allow the survival of the population, ultimately at the trait where the population growth rate $r(v)$ is maximized ($v = 1/2$). Indeed, as predicted by Theorem [4.6] this evolutionary outcome occurs for a larger set of initial conditions than when evolution is absent.

This can be seen in Figure 2b where the non-evolutionary extinction boundaries B_2^L and B_2^R lie in the shaded survival region.
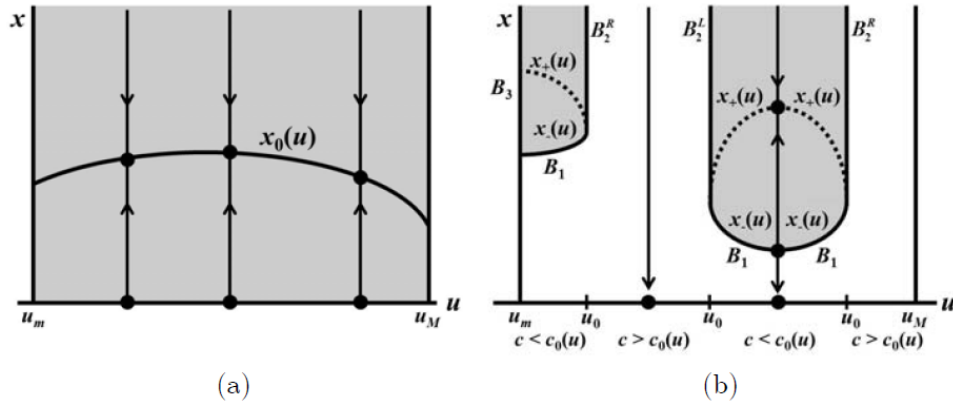

(a)   (b)

Figure 2. Sample orbits are shown for the system (6) with $r(u)$ given by (24) and parameter values $\sigma^2 = 0.01, k = 50, h = 0.5$ and $m = 4$. Extinction equilibria are $(u, x) = (0, 0), (1/2, 0)$ and $(1, 0)$.

(a) For $c = 5/2 > c(1/2) \approx 2.02$. A3 fails to hold and all orbits tend to an extinction equilibrium.

(b) For $c = 1/2 < c(1/2) \approx 2.02$. There are two survival equilibria $(x, u) \approx (1/2, 0.5251)$ and $(1/2, 7.4622)$, a saddle and stable node respectively. The shaded region is the survival region $E_{\sigma^2} = E_{0.01}$.

6. **Concluding remarks.** The ordinary differential equation (4) arises in various contexts concerning the dynamics of a biological population, for example (as we considered here) in an interaction with a predator. The equation exhibits a strong Allee effect, and hence the threat of extinction from an Allee threshold, for certain values of its coefficients. If intraspecific competition is strong (i.e., the population's carrying capacity is low), the added predation will drive the population to extinction. However, if intraspecific competition is sufficiently weak (i.e., the population's carrying capacity is large enough) the population can avoid extinction provided it maintains itself above an Allee threshold. We considered an evolutionary version of this model by assuming that the population's inherent growth rate r (the low density per capita growth rate or fitness) is determined by a phenotypic trait v that is subject to Darwinian evolution. As an evolutionary trade-off we assumed that the predator attack rate is positively correlated with the inherent growth rate, or more specifically, is proportional to it.

Using Poincaré-Bendixson theory we gave a global asymptotic analysis of the resulting evolutionary game theory model, which is a plane autonomous system with two state variables, namely, the population density and the mean phenotypic trait u. The main result of that analysis is that orbits equilibrate (i.e. there are no cycles nor cycle chains of saddles) and do so at equilibria whose mean trait components are located at critical points of $r(v)$. Survival equilibria (those with a positive population component) occur at critical traits located local maxima of $r(v)$ and they are stable provided intraspecific competition is sufficiently weak.

The second main result we obtained (Theorem 4.6) is that, under general conditions, the answer to question (22) in Section 4.2 is "yes" and to question (23) is "no". This means the extinction set, or Allee basin, (i.e., the set of population density and mean trait combinations that lead to extinction) is, when evolution occurs, a proper subset of the extinction set in the absence of evolution. In this sense, for this model at least, evolution enhances survivability by reducing the threat of an Allee threshold.

Appendix. Proof of Theorem 4.6. We begin with two lemmas.

Lemma 1. *The B_2^L and B_2^R portions of the boundary described in (13a) is either an orbit or the vector field defined by (6) when $\sigma^2 > 0$ points to the interior of S_0. In either case there is no flow across B_2^L or B_2^R.*

Proof. The B_2^L and B_2^R portions of the boundary is a vertical half line located at $u = u_0$ where $x_\pm(u)$ coalesce, i.e. thus, $c = c(u_0)$ and $x > x_0 \doteq x_-(u_0) = x_+(u_0)$. If the half line B_2^L (or B_2^R) is located at a critical point u_0, then B_2^L (or B_2^R) is an orbit and therefore there is no flow across. Suppose B_2^L or B_2^R is located at a point u_0 that is not a critical point, i.e. $\dot{r}(u_0) \neq 0$. If $\dot{r}(u_0) > 0$ then (10) implies $\dot{c}_0(u_0) > 0$ which means that the survival region S_0 lies to the right and the vertical line is a B_2^L part of the boundary. We will prove the the Lemma for this case. The proof for B_2^R when $\dot{r}(u_0) < 0$ is similar.

We need to show that at points $(u_0, x) \in B_2^L$ the vector fields point to the right, i.e. $du/dt > 0$ or, by reference to (6a), that

$$x > \frac{\sqrt{k} - 1}{hkr(u_0)}$$

for all $x > x_0$, or according to the definition of x_0, for all

$$x > \frac{hkr^2(u_0) - c_0(u_0)}{2c_0(u_0) hkr(u_0)}.$$

That this is true follows from the fact that the inequalities

$$\frac{hkr^2(u_0) - c_0(u_0)}{2c_0(u_0) hkr(u_0)} > \frac{\sqrt{k} - 1}{hkr(u_0)}$$

or equivalently

$$hkr^2(u_0) > \left(2\sqrt{k} - 1\right) c_0(u_0)$$

hold. The latter inequality is, by the definition (10) of $c_0(u)$, equivalent to

$$1 > \left(2\sqrt{k} - 1\right) \left(2k - 1 - 2\sqrt{k(k-1)}\right)$$

which is valid for all $k > 1$.   □

Lemma 2. *When $\sigma^2 > 0$ the vector field defined by (6) at non-equilibrium points of a B_1 portion of the boundary described in (13a) points into the interior of S_0.*

Proof. The B_1 portion of the boundary is defined by the curve $x = x_-(u)$ where u satisfies $c < c_0(u)$. First we note that at such points the dx/dt component of the flow vector equals 0 since $x_-(u)$ satisfies the equation (17b). Thus, the vector field is horizontal along $x_-(u)$ and our goal is to show that the component du/dt of the flow vector at a boundary point $(u, x_-(u))$ is positive when the boundary curve $x = x_-(u)$ on which it lies is decreasing and is negative when the boundary curve $x = x_-(u)$ on which it lies is increasing.

By (6a) the sign of du/dt, when $\sigma^2 > 0$, is the sign of

$$\dot{r}(u)\left(1 - \frac{k}{(1 + hkr(u)x)^2}\right).$$

We begin by proving that the second factor is positive when evaluated at points $(u, x) = (u, x_-(u))$ on the B_1.

Since $k > 1$ it follows that $k > \sqrt{k}$ and hence that

$$kr(u) > (r(u) - cx)\sqrt{k}$$

for $x \geq 0$. Evaluating this inequality at a point $(u, x) = (u, x_-(u))$ and recalling that $x_-(u) > 0$ satisfies the equation (17b), we have that

$$kr(u) > \frac{kr(u)}{1 + hkr(u)x_-(u)}\sqrt{k}.$$

Cancelling $kr(u)$ and squaring both sides of this inequality, we obtain

$$1 > \frac{k}{(1 + hkr(u)x_1(u))^2}.$$

It follows, when $\sigma^2 > 0$, that at a point $(u, x) = (u, x_-(u))$ on the boundary of B_1, the sign of the du/dt component of the flow vector is the same as the sign of $\dot{r}(u)$

$$\text{sign}\left(\frac{du}{dt}\right) = \text{sign}\ (\dot{r}(u)) \tag{25}$$

provided of course that $\dot{r}(u) \neq 0$, i.e. that u is not a critical point.

Our final step relates the sign of $\dot{r}(u)$ to the sign of the derivative $\dot{x}_-(u)$. We can re-write the equation (17b) satisfied by $x = x_-(u)$ equivalently as

$$\frac{q(u, x)}{1 + hkr(u)x} = 0$$

where

$$q(u, x) \overset{\circ}{=} (k - 1)r(u) + \left(c - hkr^2(u)\right)x + chkr(u)x^2.$$

The roots $x_-(u) < x_+(u)$ satisfy this quadratic in x and, because $q(u, x)$ defines a concave upward parabola, we see that

$$\left.\frac{dq(u, x)}{dx}\right|_{x=x_-(u)} < 0, \qquad \left.\frac{dq(u, x)}{dx}\right|_{x=x_+(u)} > 0. \tag{26}$$

An implicit differentiation of $q(u, x_-(u)) = 0$ with respect to u yields

$$\frac{\partial q(u, x_-(u))}{\partial x}\dot{x}_-(u) + \frac{\partial q(u, x_-(u))}{\partial u} = 0 \tag{27}$$

A calculation shows

$$\frac{\partial q(u, x)}{\partial u} = \frac{q(u, x) - cx - hkr^2(u)x}{r(u)}\dot{r}(u)$$

and an evaluation at the points $(u, x) = (u, x_-(u))$ yields

$$\frac{\partial q(u, x_-(u))}{\partial u} = -\frac{cx_-(u) + hkr^2(u)x_-(u)}{r(u)}\dot{r}(u)$$

so that (27) implies

$$\dot{r}(u) = \frac{\partial q(u, x_-(u))}{\partial x}\frac{r(u)}{cx + hkr^2(u)x_-(u)}\dot{x}_-(u).$$

As a result

$$\text{sign } \dot{r}(u) = \text{sign }\left(\frac{\partial q(u, x_-(u))}{\partial x}\dot{x}_-(u)\right).$$

From this and (26) we conclude

$$\begin{aligned}\text{sign } \dot{r}(u) &= -\text{sign }(\dot{x}_-(u))\\ \text{sign } \dot{r}(u) &= \text{sign }(\dot{x}_+(u))\end{aligned}$$

and from (25)

$$\text{sign }\frac{du}{dt} = -\text{sign }(\dot{x}_-(u)).$$

This shows that the component du/dt of the flow vector is positive when the boundary curve $x = x_-(u)$ is decreasing at $(u, x_-(u))$ and is negative when the boundary curve is increasing at $(u, x_-(u))$. □

Lemmas 2 and 1 show that there is no flow out of S_0 along these portions of it boundary. The only (possible) remaining portion of the boundary is a vertical half line line B_3 described by (13c), located at u_m and/or u_M. By assumption A3 both u_m and u_M are critical points and therefore B_3 is an orbit. Therefore, no flow can cross this portion of the boundary.

Proof of Theorem 4.6. By Corollary 1 any orbit in S_0 equilibrates. Since no extinction equilibrium lies in S_0, it follows that all orbits in S_0 equilibrate to a survival equilibrium. It follows that S_0 is a subset of the survival set S_{σ^2}. Since there is flow across B_2^L and B_2^R (and also possibly across B_1) into the interior of S_0, it follows that $S_{\sigma^2}\backslash S_0$ contains an open set. □

Note: A similar argument as that given in the proof of Lemma 1 shows that the flow on the curve $x = x_+(u)$ also points (at nonequilibrium points) into the interior of the region between $x_-(u)$ and $x_+(u)$.

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