Dynamics of a single species evolutionary model with Allee effects

Yun Kang\textsuperscript{1} and Oyita Udiani\textsuperscript{2}

Abstract

We investigate the evolutionary outcomes of a single species population subject to \textit{Allee effects} within the framework of a continuous strategy evolutionary game theory (EGT) model. Our model assumes a single trait creates a phenotypic trade-off between carrying capacity (i.e., competition) and predator evasion ability following a Gaussian distribution. This assumption contributes to one of our interesting findings that evolution prevents extinction even when population exhibits strong Allee effects. However, the extinction equilibrium can be an ESS under some special distributions of anti-predation phenotypes. The ratio of variation in competition and anti-predation phenotypes play an important role in determining global dynamics of our EGT model: (a) evolution may suppress strong Allee effects for large values of this ratio; (b) evolution may preserve \textit{strong Allee effects} for small values of this ratio by generating a low density evolutionary stable strategy (ESS) equilibrium which can serve as a potential Allee threshold; and (c) intermediate values of this ratio can result in multiple ESS equilibria.

\textit{Keywords:} Allee Effects, Strong/Weak Allee Effects, Evolutionary Game Theory, Evolutionary Stable Strategy (ESS), ESS Maximum Principle

1. Introduction

The Allee effect is a biological phenomenon characterized by a positive correlation between population size (or density) and the mean individual fitness (often measured as per capita growth rate) of a population or species (Courchamp \textit{et al.} 2008; Kramer \textit{et al.} 2009). Allee effects occur when species depend upon cooperative or gregarious behavior during foraging, evading natural enemies, raising their young, conditioning their environment or locating and selecting mates (Luque \textit{et al.} 2013; Tobin \textit{et al.} 2011; Dennis 1989; etc.). The role of Allee effects on population dynamics has been recognized in many biological disciplines, including population and community ecology (e.g., Dennis 1989 & 2002; Gascoigne and Lipezus 2004; Courchamp \textit{et al.} 2008; Kramer \textit{et al.} 2009; Kang and Abdul-Aziz 2012; Kang 2013), biological invasions (e.g., Drake 2004; Tobin \textit{et al.} 2011), and eco-epidemiology (e.g., Deredec and Courchamp 2006; Hilker \textit{et al.} 2009; Kang \textit{et al.} 2014).

Despite the profile of Allee effects in the population ecology and eco-epidemiology literature (e.g., see McCarthy 1997; Gyllenberg \textit{et al.} 1999; Keitt \textit{et al.} 2001; Etienne \textit{et al.} 2002; Schreiber 2003; Jang 2006; Luis \textit{et al.} 2009; Thieme \textit{et al.} 2009; Kang and Lanchier 2011; Kang and Castillo-Chavez 2014 a) there has been a limited amount of attention given toward understanding its effects in an evolutionary context. Recent work by Kanarek and Webb (2010) and Cushing and Hudson (2012) represent a positive step in this direction. Kanarek and Webb (2010) uses a spatially-explicit modeling approach that incorporates dispersal, density dependent population growth, and selection, to show that adaptive evolution may occur in small or sparse populations, providing a means of mitigating or avoiding Allee effects. Using the methods of evolutionary game theory (EGT), Cushing and Hudson

\textsuperscript{1}Sciences and Mathematics Faculty, School of Letters and Sciences, Arizona State University, Mesa, AZ 85212, USA (yun.kang@asu.edu).

\textsuperscript{2}Mathematical, Computational and Modeling Sciences Center, Arizona State University, Tempe, 85287-1904 (Oyita.Udiani@asu.edu).
(2012) investigated the global dynamics of an evolutionary model with strong Allee effects. Their results suggested that trait evolution tends to reduce the threat of extinction due to an Allee threshold.

In this paper we also use EGT methodology to study the evolutionary dynamics of a population subject to Allee effects. The model we employ here is different from the one used by Cushing and Hudson (2012) in that it is motivated specifically by Allee effects related to mating limitations and/or predation satiation. More precisely, the main goals of this manuscript are to explore the following questions:

1. In what ways does selection promote or suppress strong Allee effects when population dynamics of a species has Allee effects?

2. What are the mechanisms that can generate multiple evolutionary stable strategies (ESS) for our single species model with Allee effects?

3. What are the potential mechanisms that contribute to the extinction of species in an evolutionary setting when species is subject to Allee effects?

The rest of this paper is organized as follows. In Section 2, we derive a evolutionary model of single species with a component Allee effect induced by predator satiation and provide necessary terminologies related to evolutionary game theory that are used in this article. In Section 3, we provide sufficient conditions that lead to the ESS in different scenarios. In Section 4, we provide additional results on global dynamics of the evolutionary system and summarize global structure of dynamics based on different ranges of parameters’ values. In Section 5, we summarize our results and discuss potential biological implications of our results. Technical details and proofs appear in Section 6.

2. Model derivations

A single species population model with component Allee effects related to mating limitation or predation satiation can be described by the following model (1):

\[ x' = r x \left(1 - \frac{x}{K}\right) - \frac{ax}{hax + 1} \]

where \( r \) is the intrinsic growth rate, \( K \) is the carrying capacity of species in the absence of component Allee effects. The Holling type II functional response \( \frac{ax}{hax + 1} \) represents the positive density-dependence (i.e., component Allee effects) of an additional demographic factor, corresponding to decreases in reproduction due to a shortage of mating encounters at low population densities or decreases in mortality due to risk-dilution effects at higher population densities (Stephens and Sutherland 1999; Schreiber 2003). In the case of predation satiation, \( a, h \) respectively denote the attack rate and the handling time of predator (Denis 1989; Dercole et al. 2003). Depending on the values of \( r, a, h, K \), Model (1) can exhibit Allee effects (i.e. \( H'(0) > 0 \)), weak Allee effects (i.e., population of (1) persists with \( H'(0) > 0 \)) or strong Allee effects (i.e., \( H'(0) > 0 \) and there exists a Allee threshold above which population of (1) persists while below which population of (1) goes extinct). The following lemma summarizes its dynamics:

**Lemma 2.1.** [Dynamics of a single species model with a component Allee effect] The dynamics of Model (1) can be summarized with the following three cases:

1. If \( a < r \), then Model (1) has the following two equilibria: \( x^0 = 0 \) and

\[ x^K = \frac{|haK - 1| + \sqrt{|haK - 1|^2 + 4haK [1 - \frac{a}{r}]}}{2ha} = \frac{|haK - 1| + \sqrt{|haK + 1|^2 - \frac{4a^2hK}{r}}}{2ha} \]

where \( x^0 = 0 \) is unstable while \( x^K \) is locally asymptotically stable.
2. If \( r < a < \frac{1}{hK} \) or \( \max\{\sqrt{\frac{r}{Kh}}\left(\frac{2+\sqrt{rhK}}{4-rhK}\right), \frac{1}{hK} ; r\} < a \) and \( rhK < 4 \), then Model (1) has only the extinction equilibrium \( x^0 = 0 \) which is globally stable.

3. If the inequalities \( \frac{4}{hK} < r < a \) hold or the following inequalities hold

\[
\max\{r, \frac{1}{hK}\} < a < \sqrt{\frac{r}{Kh}}\left(\frac{2+\sqrt{rhK}}{4-rhK}\right) \text{ and } r < \frac{4}{hK},
\]

then Model (1) has the following three equilibria: \( x^0 = 0 \),

\[
x^\theta = \frac{[haK - 1] - \sqrt{[haK - 1]^2 + 4haK \left[1 - \frac{a}{r}\right]}}{2ha}
= \frac{[haK - 1] - \sqrt{[haK + 1]^2 - 4a^2hK}}{2ha}
\]

and

\[
x^K = \frac{[haK - 1] + \sqrt{[haK - 1]^2 + 4haK \left[1 - \frac{a}{r}\right]}}{2ha}
= \frac{[haK - 1] + \sqrt{[haK + 1]^2 - 4a^2hK}}{2ha}
\]

where both \( x^0 \) and \( x^K \) are locally asymptotically stable while \( x^\theta \) is unstable.

Notes: The derivative of the per capita growth rate \( H(x) \) of Model (1) can be represented as

\[
H'(x) = -\frac{r}{K} + \frac{a^2h}{(hax + 1)^2}.
\]

Therefore, Model (1) has an Allee effect whenever \( \frac{r}{K} < a^2h \) (i.e., \( a > \sqrt{\frac{r}{Kh}} \) or \( \frac{a}{r} ahK > 1 \)) holds. In addition, Lemma 2.1 implies the following three cases:

• If the attack rate \( a \) is less than the per capita growth rate \( r \), i.e., \( a < r \), then the population of species is persistent. If in addition, the inequality \( a > \sqrt{\frac{r}{Kh}} \) holds, i.e., \( \sqrt{\frac{r}{Kh}} < a < r \), then Model (1) has a weak Allee effect.

• If the attack rate \( a \) is in the intermediate range or very large, i.e. either \( r < a < \frac{1}{hK} \) or

\[
\max\{\sqrt{\frac{r}{Kh}}\left(\frac{2+\sqrt{rhK}}{4-rhK}\right), \frac{1}{hK} ; r\} < a \text{ and } rhK < 4,
\]

then the species goes extinct. Notice that

\[
a > \max\{r, \frac{1}{hK}\} \Rightarrow a/r > 1 \text{ and } ahK > 1 \Rightarrow \frac{a}{r} ahK > 1 \Rightarrow \frac{r}{K} < a^2h,
\]

thus, Model (1) can have a weak Allee effect if \( \max\{\sqrt{\frac{r}{Kh}} ; r\} < a < \frac{1}{hK} \) or \( a > \max\{r, \frac{1}{hK}\} \). This implies that even if species goes extinct, it can still have weak Allee effects.

• If the attack rate \( a \) is relatively large, i.e. either \( \frac{1}{hK} < r < a \) or:

\[
\max\{r, \frac{1}{hK}\} < a < \sqrt{\frac{r}{Kh}}\left(\frac{2+\sqrt{rhK}}{4-rhK}\right) \text{ and } r < \frac{4}{hK},
\]

holds, then the species may persist if its initial population is above a critical threshold \( x^\theta \). Otherwise, it goes extinct. According to the discussion earlier, \( x^\theta \) defines the Allee threshold. Thus, we conclude that Model (1) exhibits a strong Allee effect if \( a > \max\{r, \frac{1}{hK}\} \) holds since

\[
a > \max\{r, \frac{1}{hK}\} \Rightarrow \frac{a}{r} ahK > 1 \Rightarrow \frac{r}{K} < a^2h.
\]
We derive an evolutionary model from the ecological model (1) by following the modeling methodology for Evolutionary Game Theory (EGT) presented in Vincent and Brown (2005) (see also Rael et al. 2011; Cushing and Hudson 2012). The methodology derives equations that describe the population dynamics of \( n \) interacting species \( x_i \), together with the dynamics of (mean) phenotypic traits \( u_i \) (or strategies) which serve to characterize all individuals of a particular species and are assumed to have a heritable component. Let \( x \) denote the population densities of species and \( u \) denote a strategy used by the species which is distinct and drawn from the evolutionarily feasible traits. Then a single species \( x \) evolutionary model with a continuous strategy \( u \) has the following form:

\[
\frac{dx}{dt} = xG(v, u, x)|_{v=u} = xH(x, u)
\]

\[
\frac{du}{dt} = \sigma^2 \frac{\partial G(v, u, x)}{\partial v} |_{v=u}
\]

where \( G(v, u, x) \) is the fitness of a focal individual that chooses (or inherits) strategy (or trait) \( v \) when the population has mean trait \( u \) and density \( x \); \( H(u, x) \) denotes the fitness function for species \( x \); and \( \sigma^2 \) is a measure of the trait (or strategy) variance present in species \( x \) around the mean trait \( u \).

In the rest of this article, we take \( x(t) \) as the population density of a prey that is subject to a generalist predator with Holling Type II functional response (i.e., predator saturation); and \( u(t) \) as a phenotypic trait that is related to prey’s competitive performance measured by its carrying capacity \( K(u) \) and anti-predation behavior measured by \( a(u) \). The extended evolutionary model from the ecological model (1) has the following form:

\[
\frac{dx}{dt} = xG(v, u, x)|_{v=u} = x \left[ r \left( 1 - \frac{x}{K(u)} \right) - \frac{a(u)}{1+ha(x)} \right] = xH(x, u)
\]

\[
\frac{du}{dt} = \sigma^2 \frac{\partial G(v, u, x)}{\partial v} |_{v=u} = \sigma^2 u \left[ -\frac{rx}{\sigma^2 K(u)} + \frac{a}{\sigma^2 (1+ha(x))} \right],
\]

\[
K(u) = K_0 e^{-\frac{u^2}{2\sigma^2_k}}; \quad a(u) = a_0 e^{-\frac{u^2}{2\sigma^2_a}}
\]

where \( G(v, u, x) = r \left( 1 - \frac{x}{K(u)} \right) - \frac{a(v)}{1+ha(v)x} \) and \( K(u) \) varies with prey trait \( u \) which follows a Gaussian distribution \( N(0, \sigma^2_k) \). This formulation assumes the maximum equilibrium level \( K_0 \) for prey species \( x \), using strategy \( u \), in the absence of predation is attained at trait \( u = 0 \), and that \( K(u) \) is normally distributed around \( u = 0 \) with variance \( \sigma^2_k \). Similarly, we assume that the predation efficiency is discounted by anti-predation behavior \( a(u) \) which is normally distributed around a maximum value of \( a_0 \) with a variance \( \sigma^2_a \). Notice that both \( K(u) \) and \( a(u) \) are even functions of \( u \), are decreasing with respect with \( u > 0 \), and are increasing with respect with \( u < 0 \). The larger the trait value \( |u| \), the smaller values of \( K(u) \) and \( a(u) \) which indicates an inherent trade-off between the prey’s ability to compete for resources and avoid being killed by predators. In addition, we assume that other parameters (i.e., the intrinsic growth rate of prey \( r \) and the predator handling time \( h \) are not influenced by the quantitative traits \( u \).

**Evolutionary Stable Strategy (ESS):** The ESS concept was first introduced by Maynard-Smith and Price (1973) which provides evolutionary game theory with a solution concept for identifying possible outcomes of natural selection (Brown et al. 2007). Maynard-Smith (1982) originally described an ESS as a strategy or set of strategies, which, when common, cannot be invaded by any rare alternative strategies. This property of an ESS can be stated in terms of the ESS maximum principle which ensures that a population at an ESS is resistant to invasion (Vincent and Brown 1988). In this paper, we define \( u^* \) is an ESS if the equilibrium \((x^*, a^*)\) with \( x^* > 0 \) of the evolutionary model (3) if \((x^*, a^*)\) is locally asymptotically stable and satisfies **ESS maximum principle**, i.e.,

\[
\max_{v \in \mathbb{R}} \{ G(v, u^*, x^*) \} = G(u^*, u^*, x^*) = 0.
\]
Even though there is no real biological meaning to define an ESS when \( x^* = 0 \), we define that \((0, u^*)\) is an ESS if it is locally asymptotically stable and satisfies (5).

\[
\max_{v \in \mathbb{R}} \{ G(v, u^*, 0) \} \leq 0. \tag{5}
\]

In the next section, we will investigate the detailed evolutionary dynamics of Model (3).

3. Evolutionary dynamics of a single species model with Allee effects

Suppose we define:

\[
\phi(a_0) = \frac{\sigma_a \left[ \frac{1}{2rh} - \frac{1}{ha_0} + \frac{\sqrt{1 + 4r\sigma_k^2/(a_0\sigma_z^2)}}{2rh} \right] 1 + \sqrt{1 + \frac{4r\sigma_k^2}{a_0\sigma_z^2}}}{4r^2h\sigma_K^2}, \tag{6}
\]

then we have the following proposition regarding the equilibrium of the evolutionary model (3):

**Proposition 3.1** (The equilibria of Model (3)). The evolutionary model (3) always has the extinction equilibrium \((0, 0)\). If \( a_0 < \frac{r}{1 + (\frac{r}{4})^2} \), then Model (3) has only two equilibria: \((0, 0)\) and \((x^K(0), 0)\). The evolutionary model (3) has at least five equilibria: \((0, 0), (x^0(0), 0), (x^K(0), 0)\), and \((x^*, \pm u^*)\) where \(|x^*u^*| > 0\) if either

\[
\max\left\{ \frac{r}{K_0h} \left( \frac{2 + \sqrt{hK_0}}{4 - rhK_0} \right), \frac{1}{hK_0}, r \right\} < a_0 \text{ and } \frac{1}{ha_0} < K_0 < \min\{\phi(a_0), \frac{rh}{4}\}
\]

or the inequalities \(\max\{\frac{1}{ha_0}, \frac{4}{hr}\} < K_0 < \phi(a_0), r < a_0\) hold.

**Notes:** Proposition 3.1 provides \(K_0 < \phi(a_0)\) as a sufficient condition to guarantee the existence of an interior equilibrium. However, if (11) does not hold, i.e., \(K(0) = K_0 \geq \phi(a_0)\), then the evolutionary model (3) may have none or two interior equilibria. According to the expression of \(\phi(a_0)\), we suggest that \(K_0 < \phi(a_0)\) can hold if the ratio \(\frac{(\frac{\sigma_k}{\sigma_a})^2}{\sigma_a^2}\) is sufficiently small or large:

1. When \(\left(\frac{\sigma_k}{\sigma_a}\right)^2\) is small, then we have

\[
\phi(a_0) = \frac{\sigma_a \left[ \frac{1}{2rh} - \frac{1}{ha_0} + \frac{\sqrt{1 + 4r\sigma_k^2/(a_0\sigma_z^2)}}{2rh} \right] 1 + \sqrt{1 + \frac{4r\sigma_k^2}{a_0\sigma_z^2}}}{4r^2h\sigma_K^2} > \frac{1}{2rh} - \frac{1}{ha_0} + \frac{\sqrt{1 + \frac{4r\sigma_k^2}{a_0\sigma_z^2}}}{2rh},
\]

which can be larger than \(K_0\). In this case, Model (3) can have one interior equilibrium \((x^*, u^*)\).

2. When \(\left(\frac{\sigma_k}{\sigma_a}\right)^2\) is large, then we have

\[
\phi(a_0) = \frac{\sigma_a \left[ \frac{1}{2rh} - \frac{1}{ha_0} + \frac{\sqrt{1 + 4r\sigma_k^2/(a_0\sigma_z^2)}}{2rh} \right] 1 + \sqrt{1 + \frac{4r\sigma_k^2}{a_0\sigma_z^2}}}{4r^2h\sigma_K^2} > \frac{1}{2rh} - \frac{1}{ha_0} + \frac{\sqrt{1 + \frac{4r\sigma_k^2}{a_0\sigma_z^2}}}{2rh},
\]

which can be larger than \(K_0\). Thus, Model (3) can have one interior equilibrium \((x^*, u^*)\).
Since \( a(u) \), \( K(u) \) and \( \phi(a(u)) \) are even functions with respect with \( u \), thus, if \((x^*, u^*)\) is an interior equilibrium of the evolutionary model (3), so is \((x^*, -u^*)\). This implies that the evolutionary model (3) always has even number of interior equilibria. Simulations confirm that Model (3) can have up to four interior equilibria: either two \((x^\theta(\pm u^\theta), \pm u^\theta)\) and two \((x^K(\pm u^K), \pm u^K)\) or four \((x^K(\pm u^K), \pm u^K)\). Condition (11) guarantees the existence of interior equilibrium \((x^\theta(\pm u^\theta), \pm u^\theta)\) which could be \((x^\theta(\pm u^\theta), \pm u^\theta)\) or \((x^K(\pm u^K), \pm u^K)\). Define the following ecological model (7)

\[
x' = x \left[ r(1 - \frac{x}{K(u^*)}) - \frac{a(u^*)}{1 + h a(u^*) x} \right].
\]

For convenience, we define the following terminology for the rest of this manuscript:

1. Assume that the ecological model (7) has a strong Allee effect
   
   (a) **Allee threshold equilibrium**: We define \((x^\theta(\pm u^\theta), \pm u^\theta)\) as the boundary Allee threshold equilibrium if \(u^\theta = 0\) and as the interior Allee threshold equilibrium if \(u^\theta \neq 0\).
   
   (b) **Strong Allee effect equilibrium**: We define \((x^K(\pm u^K), \pm u^K)\) as the boundary strong Allee effect equilibrium if \(u^K = 0\) and as the interior strong Allee effect equilibrium if \(u^K \neq 0\).
   
   (c) Similarly, we can define \((x^K(u^K), u^K)\) as a boundary/interior strong Allee effect ESS if \((x^K(u^K), u^K)\) is ESS.

2. Assume that the ecological model (7) has a weak Allee effect,
   
   (a) **Weak Allee effect equilibrium**: We define \((x^K(\pm u^K), \pm u^K)\) as the boundary weak Allee effect equilibrium if \(u^K = 0\) and as the interior weak Allee effect equilibrium if \(u^K \neq 0\).
   
   (b) Similarly, we can define \((x^K(u^K), u^K)\) as a weak Allee effect ESS if \((x^K(u^K), u^K)\) is an ESS.

3. **The carrying capacity equilibrium**: We define a weak Allee effect equilibrium or a strong Allee effect equilibrium (i.e., \((x^K(u^K), u^K)\)) as the carrying capacity equilibrium. More specifically, we can also call \((x^K(0), 0)\) as the boundary carrying capacity equilibrium and \((x^K(u^K), u^K)\) as the interior carrying capacity equilibrium.

Proposition 3.1 implies that if (11) holds, then Model (3) has interior equilibria \((x^*, \pm u^*)\) with \(u^* \neq 0\) where either \(f(a(u^*)) = x^K(u^*)\) or \(f(a(u^*)) = x^\theta(u^*)\). We have the following two scenarios:

1. If \(x^\theta(u^*) > 0\) and \(K(u^*) > 2f(a(u^*) + \frac{1}{ha(u^*)}), \) then \(u^*\) has to satisfy the equation \(f(a(u^*)) = x^\theta(u^*)\) since

\[
\frac{[ha(u^*)K(u^*) - 1] - \sqrt{[ha(u^*)K(u^*) - 1]^2 + 4ha(u^*)K(u^*) \left[ 1 - \frac{a(u^*)}{r} \right]}}{2ha(u^*)} = f(a(u^*)) < \frac{K(u^*)}{2} - \frac{1}{2ha(u^*)}.
\]

2. If \(x^K(u^*) > 0\) and \(K(u^*) < 2f(a(u^*) + \frac{1}{ha(u^*)}), \) then \(u^*\) has to satisfy the equation \(f(a(u^*)) = x^K(u^*)\) since

\[
\frac{[ha(u^*)K(u^*) - 1] + \sqrt{[ha(u^*)K(u^*) - 1]^2 + 4ha(u^*)K(u^*) \left[ 1 - \frac{a(u^*)}{r} \right]}}{2ha(u^*)} > \frac{K(u^*)}{2} - \frac{1}{2ha(u^*)}.
\]

The following theorem provides results on the equilibrium \((x^*, u^*)\) of Model (3) and its stability:
Theorem 3.1 (Equilibria and their stability of Model (3)). The trivial equilibrium \((0, 0)\) is always unstable; The boundary equilibrium \((x^0(0), 0)\) is always unstable if it exists; and the boundary equilibrium \((x^K(0), 0)\) exists if \(r > a_0\) or \(\frac{4}{hK_0} < r < a_0\) or

\[
\max\{r, \frac{1}{hK_0}\} < a_0 < \sqrt{\frac{r}{K_0 h} \left(\frac{2}{4 - rhK_0} \right)} \quad \text{and} \quad r < \frac{4}{hK_0}.
\]

If \((x^K(0), 0)\) exists, then it is locally asymptotically stable if the inequality \(\frac{\sigma^2_K}{\sigma^2_u} < h a_0 x^K(0)\) holds. The evolutionary model \((3)\) always has an even number of interior equilibria, i.e., if \((x^*, u^*)\) is an interior equilibrium so is \((x^*, -u^*)\). The detailed stability condition of the equilibrium of the evolutionary model \((3)\) is listed in Table 1.

<table>
<thead>
<tr>
<th>Equilibrium</th>
<th>Sufficient Condition for Existence</th>
<th>Stability</th>
</tr>
</thead>
<tbody>
<tr>
<td>((0, 0))</td>
<td>Always</td>
<td>Saddle if (r &lt; a_0); Source if (r &gt; a_0).</td>
</tr>
<tr>
<td>((x^0(0), 0))</td>
<td>Either (\frac{1}{hK_0} &lt; r &lt; a_0) or (\max{r, \frac{1}{hK_0}} &lt; a_0 &lt; \sqrt{\frac{r}{K_0 h} \left(\frac{2}{4 - rhK_0} \right)} ) and (r &lt; \frac{4}{hK_0})</td>
<td>It is a saddle if (\frac{\sigma^2_K}{\sigma^2_u} &lt; h a_0 x^0(0)(1+ha_0 x^0(0))^2) while it is a source if (\frac{\sigma^2_K}{\sigma^2_u} &gt; h a_0 x^0(0)).</td>
</tr>
<tr>
<td>((x^K(0), 0))</td>
<td>Either (r &gt; a_0) or (\max{r, \frac{1}{hK_0}} &lt; a_0 &lt; \sqrt{\frac{r}{K_0 h} \left(\frac{2}{4 - rhK_0} \right)} ) and (r &lt; \frac{4}{hK_0})</td>
<td>It is locally asymptotically stable if (\frac{\sigma^2_K}{\sigma^2_u} &lt; h a_0 x^K(0)) while it is a saddle if (\frac{\sigma^2_K}{\sigma^2_u} &gt; h a_0 x^K(0)(1+ha_0 x^K(0))^2).</td>
</tr>
<tr>
<td>((x^0(u^0), u^0))</td>
<td>(K_0 &lt; \phi(a_0)) and (K(u^0) &gt; 2f(a(u^0)) + \frac{1}{ha(u^0)})</td>
<td>It is a saddle if (\frac{\sigma^2_K}{\sigma^2_u} &lt; \frac{1+ha^* x^0}{ha^* x^0 - 1}) holds while it is a source if (\frac{\sigma^2_K}{\sigma^2_u} &lt; \min{\frac{1+ha^* x^0}{ha^* x^0 - 1}, \sqrt{\frac{a^* x^0}{ha^* x^0 - 1}}}).</td>
</tr>
<tr>
<td>((x^K(u^K), u^K))</td>
<td>(K_0 &lt; \phi(a_0)) and (K(u^K) &lt; 2f(a(u^K)) + \frac{1}{ha(u^K)})</td>
<td>It is locally asymptotically stable if either (\frac{\sigma^2_K}{\sigma^2_u} &gt; \frac{ha^* x^K - 1}{1+ha^* x^K}) or (\frac{\sigma^2_K}{\sigma^2_u} &lt; \frac{a^* x^K(1+ha^* x^K)}{ha^* x^K - 1}) holds while it is a saddle if (\frac{\sigma^2_K}{\sigma^2_u} &lt; \frac{1+ha^* x^K}{ha^* x^K - 1}).</td>
</tr>
</tbody>
</table>

Table 1: The local stability of equilibria for Model (3). Note that \(f(x) = \frac{1}{2rK} + \frac{1}{hx} + \sqrt{\frac{1+4r\sigma^2_K/(\sigma^2_u)}{2rh}}\) and \(\phi(x) = \frac{\sigma^2_K}{\sigma^2_u} \frac{1+4r\sigma^2_K/(\sigma^2_u)}{4r^2 ha_0 x^K} \).

Notes: Theorem 3.1 suggests the following scenarios for the single species evolutionary model (3)

1. When \(\left(\frac{\sigma^2_K}{\sigma^2_u}\right)^2\) is small, then Model (3) can have interior equilibria \((x^*, \pm u^*)\) according to Proposition 3.1. In this case, if the boundary weak Allee effect equilibrium \((x^0(0), 0)\) and/or the weak Allee effect equilibrium \((x^0(u^0), u^0)\) exist, then they are saddles. Conversely, if the boundary carrying capacity equilibrium \((x^K(0), 0)\) and/or the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) exist, then they are sinks. In addition, small values of \(\left(\frac{\sigma^2_K}{\sigma^2_u}\right)^2\) generates the potential multiple attractors in Model (3).
2. When \( \left( \frac{\sigma K}{\sigma a} \right)^2 \) is large, then Model (3) can have interior equilibria \((x^*, \pm u^*)\) according to Proposition 3.1. In this case, we have the following sub-cases

(a) If the boundary Allee threshold equilibrium \((x^0(0), 0)\) exists, then it is a source. If the interior Allee threshold equilibrium \((x^0(u^0), u^0)\) exists, then it is also a source when \( ha^* x^0(u^0) > 1 \) while it is a saddle when \( ha^* x^0(u^0) < 1 \).

(b) If the boundary carrying capacity equilibrium \((x^K(0), 0)\) exists, then it is a saddle. If the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) exists, then it is also a saddle when \( ha^* x^K(u^K) > 1 \). Otherwise, it is a sink (i.e., it is locally asymptotically stable) when \( ha^* x^K(u^K) < 1 \).

3. We suspect that it is impossible for the equilibrium \((x^*, u^*)\) to go through a Hopf bifurcation, thus Model (3) should have simple equilibrium dynamics.

Therefore, if the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) exists, it can be locally asymptotically stable when \( \left( \frac{\sigma K}{\sigma a} \right)^2 \) is small enough or when \( \left( \frac{\sigma K}{\sigma a} \right)^2 \) is large enough but \( ha^* x^K(u^K) < 1 \). However, the boundary carry capacity equilibrium \((x^K(0), 0)\) can be locally stable only if the value of \( \left( \frac{\sigma K}{\sigma a} \right)^2 \) is not too large. From Proposition 3.1, we also know that if \((x^K(u^K), u^K)\) is a locally stable equilibrium then so is \((x^K(-\theta K), -\theta K)\). The following case provides a case when Model (3) has multiple attractors. For example, if we take \( K_0 = 2, a_0 = 0.35, \sigma_K = 0.5, \sigma_a = 0.35, r = 0.25, h = 9.5 \), then Model (3) have the following seven equilibria:

\[
(0, 0), \ (0.1559, 0), \ (1.5434, 0), \ (0.4070, \pm 2.7516), \ (0.0877, \pm 4.6500)
\]

where \((1.5434, 0)\) and \((0.0877, \pm 4.6500)\) are locally asymptotically stable.

As discussed earlier, a sufficient condition for \((x^*, u^*)\) to be an ESS is that it is locally asymptotically stable and satisfies ESS maximum principle (4). The following theorem provides results on the ESS of Model (3) when \( u^* = 0 \):

**Theorem 3.2** (ESS of the single species evolutionary model). Assume that

\[
r > a_0
\]

or

\[
\frac{4}{h K_0} < r < a_0
\]

or

\[
\max \{ r, \frac{1}{h K_0} \} < a_0 < \sqrt{\frac{r}{K_0 h} \left( \frac{2 + \sqrt{r h K_0}}{4 - r h K_0} \right)} \quad \text{and} \quad r < \frac{4}{h K_0}
\]

holds. Then the boundary carrying capacity equilibrium \((x^K(0), 0)\) is an ESS if one of the following inequality holds:

1. \( \frac{\sigma K}{\sigma_a^2} \leq \min \left\{ \frac{r x^K(0)}{a_0 h a_0}, h a_0 x^K(0) \right\} \) or

2. \( \frac{\sigma K}{\sigma_a^2} \leq \max \left\{ 1, \min \left\{ \frac{r a_0 h^2 (x^K(0))^3}{K_0}, h a_0 x^K(0) \right\} \right\} \).

**Notes:** Theorem 3.2 provides sufficient conditions for the boundary carrying capacity equilibrium \((x^K(0), 0)\) to be an ESS of Model (3) when \( \frac{\sigma K}{\sigma_a^2} \) is sufficiently small. The following theorem states that if the inequality \( \frac{\sigma K}{\sigma_a^2} < \frac{r}{a_0} - 1 \) holds, i.e., the values of \( \frac{\sigma K}{\sigma_a^2} \) is small and the ecological dynamics of (3) has no strong Allee effects \((r > a_0)\), then \((x^K(0), 0)\) is always an ESS.
Theorem 3.3 (Boundary ESS of the single species evolutionary model (3)). If \( \frac{\sigma_a^2}{\sigma_a^2} < \frac{r}{\sigma_a} - 1 \), then the boundary carrying capacity equilibrium \((x^K(0), 0)\) is the only locally asymptotically stable equilibrium which is also an ESS.

Notes: Both Theorem 3.2 and Theorem 3.3 imply that the boundary carrying capacity equilibrium \((x^K(0), 0)\) is an ESS of Model (3) if the values of \( \frac{\sigma_a^2}{\sigma_a^2} \) is small enough. Theorem 3.1 and its notes suggest the Model (3) can have multiple locally asymptotically stable equilibria whenever \( \frac{\sigma_a^2}{\sigma_a^2} \) is small enough. One question of interest is that if \((x^K(0), 0)\) is an ESS, can Model (3) also have an ESS interior carrying capacity equilibrium \((x^K(u^K), u^K)\)? The following theorem provides sufficient conditions for this case:

Theorem 3.4 (Interior ESS of the single species evolutionary model (3)). Assume that the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) is locally asymptotically stable, then it is an ESS if \(x^K(u^K) < \frac{1}{2a_0h} \) and either

\[
\frac{\sigma_a^2}{\sigma_a^2} \leq \frac{r x^* e^{\frac{(\sigma_a^*)^2}{2 \sigma_a^2} \left(1 + \frac{\sigma_a^2}{2 \sigma_a^2} \right)}}{a_0 K_0}
\]

or

\[
\frac{\sigma_a^2}{\sigma_a^2} \leq \max \left\{ 1, \frac{r a_0 h^2 (x^*)^3 e^{\frac{(\sigma_a^*)^2}{2 \sigma_a^2} \left(1 - \frac{\sigma_a^2}{2 \sigma_a^2} \right)}}{K_0} \right\}
\]

holds.

Notes: Combined the results from Theorem 3.1 and Theorem 3.4, we can conclude that Model (3) has two interior ESS \((x^K(u^K), u^K)\) and \((x^K(-u^K), -u^K)\) if the following conditions are satisfied:

- The inequality (11) (i.e., \( K_0 < \phi(a_0) \)) holds, which guarantees the existence of the interior equilibrium \((x^*, u^*)\).
- The inequality \( K(u^K) < 2 f(a(u^K)) + \frac{1}{ha(u^K)} \) holds, which guarantees that \((x^*, u^*)\) is in fact the interior carrying capacity equilibrium \((x^K(u^K), u^K)\).
- Either the inequality (18) (i.e., \( \frac{\sigma_a^2}{\sigma_a^2} > \frac{ha^*_x x^K - 1}{1 + ha^*_x x^K} \)) or the inequality (19) (i.e., \( \left(\frac{\sigma_a^2}{\sigma_a^2}\right)^2 > \frac{ha^*_x x^K - 1}{1 + ha^*_x x^K} \)) holds. This condition guarantees that the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) is locally asymptotically stable.
- Either the inequality \( \frac{\sigma_a^2}{\sigma_a^2} \leq \frac{r x^* e^{\frac{(\sigma_a^*)^2}{2 \sigma_a^2} \left(1 + \frac{\sigma_a^2}{2 \sigma_a^2} \right)}}{a_0 K_0} \) or \( \frac{\sigma_a^2}{\sigma_a^2} \leq \max \left\{ 1, \frac{r a_0 h^2 (x^*)^3 e^{\frac{(\sigma_a^*)^2}{2 \sigma_a^2} \left(1 - \frac{\sigma_a^2}{2 \sigma_a^2} \right)}}{K_0} \right\} \) holds. This condition guarantees that the interior carrying capacity equilibrium \((x^K(u^K), u^K)\) satisfies the ESS maximum principle.

In addition, it is possible for Model (3) to have the boundary carrying capacity equilibrium \((x^K(0), 0)\) and the interior carrying capacity equilibrium \((x^K(\pm u^K), \pm u^K)\) as the ESS for given values of \(r, a_0, K_0, h, \sigma_K, \sigma_a\). For example, if we take \( K_0 = 2, a_0 = 0.35, \sigma_K = .2, \sigma_a = .5, r = .25, h = 9.5 \), then Model (3) have the following seven equilibria:

\((0, 0), (0.1559, 0), (1.5434, 0), (0.154315, \pm 0.135), (0.0165, \pm 0.485)\)

where \((1.5434, 0)\) and \((0.0165, \pm 0.485)\) are ESS (see Figure 1). Here we would like to point out that the fitness function \(G(v, u^K, x^K)\) of the interior Allee threshold equilibria \((x^K(\pm u^K), \pm u^K)\) can have global maximum at \((x^K(\pm u^K), \pm u^K)\) (i.e., they satisfy the ESS maximum principle) even though these interior equilibria are sources.
conditions on (0 examples in Cushing and Hudson 2010). In this subsection, we provide a proposition regarding sufficient

Figure 1: The equilibria of single species evolutionary model (3) and their ESS status when

4. Global Dynamical Structures and Numerical Simulations

The population density of species \( x \) is bounded by \( K_0 \) provided that \( K(u) = K_0 e^{-\frac{a}{2K}}. \) However, the evolutionary model (3) may be unbounded due to the fact that \( u'\Big{|}_{x=0,u>0} = \frac{a(u)u}{\sigma_a} > 0 \) and \( u'\Big{|}_{x=0,u<0} = \frac{a(u)u}{\sigma_a} < 0. \) The following proposition 4.1 and Proposition 3.1 as well as related numerical simulations suggest that the evolutionary model (3) has on limit cycles, i.e., only equilibrium dynamics.

**Proposition 4.1** (*No limit cycles*) The evolutionary model (3) only has equilibrium dynamics if

\[ r > \max \left\{ hK_0a_0^2 \left( \frac{\sigma_K}{\sigma_a} \right)^4 hK_0a_0^2 \right\}. \]

**Notes:** The notes of Lemma 2.1 implies that the inequality \( r < ha(u)^2K(u) \leq ha_0^2K_0 \) is the condition for the ecological dynamics of Model (3) having Allee effects. However, Proposition 4.1 indicates that Model (3) has only equilibrium dynamics whenever it has no Allee effects, i.e., the condition \( r > \max \left\{ hK_0a_0^2 \left( \frac{\sigma_K}{\sigma_a} \right)^4 hK_0a_0^2 \right\} \) hold. In addition, our simulations suggest that Model (3) has equilibrium dynamics for all ranges of parameters values. This is consistent with Proposition 3.1 which suggests that limit cycles is impossible since there are no Hopf bifurcations. Both analytic and simulation results suggest the equilibrium dynamics for all values of parameters, which is similar to the study by Cushing and Hudson (2012).

**4.1. Extinction equilibrium**

The model (3) assumes that \( K(u) = K_0 e^{-\frac{a}{2K}}; \) \( a(u) = a_0 e^{-\frac{u^2}{2\sigma_a}}. \) Under this assumption, our analysis suggests that the extinction equilibrium \((0, u^*)\) will never be locally asymptotically stable. In other words, evolution prevents deterministic extinction. This is different from the result stated in Cushing and Hudson (2012). One possible explanation for this difference is that the extinction of a species can tie to the formations of \( K(u) \) and \( a(u) \). In nature, \( K(u) \) or \( a(u) \) can have different forms (see various examples in Cushing and Hudson 2010). In this subsection, we provide a proposition regarding sufficient conditions on \((0, u^*)\) that guarantee its local asymptotic stability (and evolutionary stability) when both \( K(u) \) and \( a(u) \) have general forms.
Proposition 4.2 (ESS extinction equilibrium). Assume that \( K(u) \) and \( a(u) \) are smooth and strictly positive equations in \( u \). Then \((0, u^*)\) is an ESS extinction equilibrium of the evolutionary model (28) if the following inequalities are satisfied:

\[
a'(u^*) = 0, \ a''(u^*) > 0 \text{ and } r < a(u^*) \leq \max_{v \in \mathbb{R}} \{a(v)\}. \]

Notes: Proposition 4.2 implies that the maximum growth rate \( r \) and the anti-predation ability \( a(u) \) determine whether \((0, u^*)\) is an ESS or not. However, the carrying capacity \( K(u) \) does not have any effect on neither the existence nor stability. For example, if we take \( a(u) = a_0 - e^{-\frac{u^2}{\sigma^2}} \) (see Cushing and Hudson 2012), then \( a'(u^*) = 0 \) gives \( u^* = 0 \). Since \( a''(0) = \frac{2}{\sigma^2} > 0 \), then we can conclude that \((0, 0)\) is locally asymptotically stable if \( r < a_0 - 1 \). In this case, we have

\[
\max_{v \in \mathbb{R}} \{G(v, u^*, x^*)\} = \max_{v \in \mathbb{R}} \{r - a(v)\} = \max_{v \in \mathbb{R}} \{r - a_0 + e^{-\frac{u^2}{\sigma^2}}\} = G(0, 0, 0) = r - a_0 + 1 < 0.
\]

Therefore, we can conclude that \((0, 0)\) is an ESS of Model (28) if \( a(u) = a_0 - e^{-\frac{u^2}{\sigma^2}} \) and \( r < a_0 + 1 \). If we also assume that the maximum growth rate \( r \) is a smooth and strictly positive function of \( u \), then the Darwinian dynamics (2) can be rewritten as follows by assuming general forms of \( K(u), a(u) \):

\[
\frac{dx}{dt} = xG(v, u, x) \big|_{v = u} = x \left[ r(u) \left( 1 - \frac{x}{K(u)} \right) - \frac{a(u)}{1 + hax(u)x} \right] = xH(u, x) \tag{8}
\]

\[
\frac{du}{dt} = \sigma^2 \frac{\partial G(v, u, x)}{\partial v} \big|_{v = u} = \sigma^2 \left[ \frac{r(u)xK'(u)}{K^2(u)} - \frac{a'(u)}{(1 + hax)^2} + r'(u)(1 - \frac{x}{K(u)}) \right].
\]

Thus \((0, u^*)\) is an equilibrium of (8) if \( a'(u^*) = r'(u^*) \). The stability of \((0, u^*)\) is determined by the eigenvalues of the following Jacobian matrix evaluated at \((0, u^*)\)

\[
J(x^*, u^*) \bigg|_{x^* = 0} = \begin{bmatrix}
0 & \sigma^2 \left[ \frac{rK'(u^*)}{K^2(u^*)} + 2ha(u^*)a'(u^*) - \frac{r(u^*)}{K(u^*)} \right] \\
\sigma^2 \frac{rK'(u^*)}{K^2(u^*)} & -\sigma^2 [a''(u^*) - r''(u^*)]
\end{bmatrix}
\]

Then the following proposition provides a sufficient condition for \((0, u^*)\) being an ESS extinction equilibrium of (8)

Proposition 4.3 (ESS extinction equilibrium). Assume that \( a(u) \), \( K(u) \) and \( r(u) \) are smooth and strictly positive equations in \( u \). Then \((0, u^*)\) is an ESS extinction equilibrium of the evolutionary model (8) if the following inequalities are satisfied:

\[
a'(u^*) = r'(u^*), \quad a''(u^*) > r''(u^*) \text{ and } \max_{v \in \mathbb{R}} \{G(v, u^*, 0)\} = \max_{v \in \mathbb{R}} \{r(v) - a(v)\} < 0.
\]

We define the ESS condition for the extinction equilibrium \((0, u^*)\) as before (i.e. locally asymptotically stable and satisfies (5)) even through it may not be biological motivated. In this subsection, we have provided sufficient conditions under which the extinction equilibrium \((0, u^*)\) is an ESS of Model (2) when the maximum growth rate \( r \), the anti-predation ability \( a \) and the carrying capacity \( K \) have general forms of the trait \( u \). Our study suggests that alternate forms of \( r(u) \) and \( a(u) \) can force the extinction equilibrium \((0, u^*)\) to become an ESS of Model (2). Conversely, the carrying capacity \( K(u) \) has no such effects on the existence and stability of \((0, u^*)\).

4.2. Global structure of dynamics

In this subsection, we summarize analytical results obtained from the previous sections and perform numerical simulations to support our findings. We summarize the global dynamics structure of Model (3) as follows based on the values of \( r, a_0, K_0, h \) and \( \frac{\sigma^2}{\sigma^2} \).


1. **Equilibrium Dynamics**: Theorem 3.1 and Proposition 4.1 as well as numerical simulations suggest that there is no limit cycle for Model (3) since the only possible source is the boundary Allee threshold equilibrium \((x^\theta(0), 0)\) which is never stable. Thus, Model (3) has simple equilibrium dynamics.

2. **No Extinction**: Model (3) assumes that \(a(u)\) is normally distributed around \(u = 0\) with variance \(\sigma_a^2\), respectively (i.e., \(a(u) = a_0 e^{-\frac{u^2}{2\sigma_a^2}}\)). This assumption leads to the results that the extinction equilibrium \((0, 0)\) is always unstable, suggesting that species evolution can prevent deterministic extinction. However, this result may not hold if \(a(u)\) has a different distributional form with respect to \(u\) according to Proposition 4.2. In fact, it is possible for the extinction \((0, 0)\) to be an ESS under certain distributions of \(r(u)\) and \(a(u)\) while the distribution of \(K(u)\) has no effect in determining the stability of \((0, 0)\).

3. **Evolution may promote the existence of the interior carrying capacity equilibrium** \((x^K(u^K), u^K)\) under certain conditions. The maximum values of \(K(u)\) and \(a(u)\) are \(K_0, a_0\) at \(u = 0\), respectively. According to Lemma 2.1, species goes extinct at \(u = 0\) if \(r < a_0 < \frac{1}{K_0} h\) or

\[
\max\left\{ \frac{r}{K_0 h} \left( \frac{2 + \sqrt{r h K_0}}{4 - r h K_0} \right), \frac{1}{h K_0}, r \right\} < a_0 \text{ and } r h K_0 < 4.
\]

However, as traits evolve, numerical simulations suggest that Model (3) always has two symmet-

![Figure 2: Schematic phase plane for System (3) when there is extinction at \(u = 0\). The green, blue dots denote the equilibria are saddle nodes, stable nodes, respectively.](image)

4. **The ratio** \(\frac{\sigma_K^2}{\sigma_a^2}\) **plays an important role in determining the global dynamics of Model (3):**

   (a) **Small values of** \(\frac{\sigma_K^2}{\sigma_a^2}\):

   i. **No Strong Allee Effects** if \(r > a_0\): According to Lemma 2.1 and its associated notes, we can conclude that the evolutionary model (3) does not have an Allee effect
equilibrium \((x^*, u^*)\) if \(r > a_0\) since \(a_0 \geq a(u)\). However, Model (3) can still have a weak Allee effect equilibrium or even a weak Allee effect ESS under certain conditions. For example, if \(\sqrt{\frac{r}{hK}} < a_0 < r\), then Model (3) has the boundary weak Allee effect equilibrium \((x^K(0), 0)\) which is an ESS when the inequality \(\sigma^2_K < \frac{r}{hK} - 1\) holds according to Theorem 3.3 (see Figure 3(a) for the dynamical structure of this case).

ii. **Multiple Attractors if** \(r < a_0\): According to Theorem 3.1, Theorem 3.2, Theorem 3.4, we know that if the boundary carrying capacity equilibrium \((x^K(0), 0)\) and the interior carrying capacity equilibria \((x^K(\pm u^K), \pm u^K)\) exist, then they are locally asymptotically stable which are also ESS if additional conditions are satisfied. In this case, the boundary Allee threshold \((x^K(0), 0)\) is a saddle whose stable manifold separates the basins of attractions of \((x^K(0), 0)\) and \((x^K(\pm u^K), \pm u^K)\) (see Figure 3(b) for the dynamical structure of this case). An important point to note is that if the values of \(\frac{\sigma^2_K}{\sigma^2_u}\) are extremely small, the interior carrying capacity equilibria \(x^K(\pm u^K)\) tends to be very small too. In this case, chances of perturbations may drive the species to extinction since this equilibrium can serve as an artificial Allee threshold.

![Schematic phase plane for System (3) when \(r > a_0\).](image1)

![Schematic phase plane for System (3) when \(r < a_0\).](image2)

**Figure 3**: Schematic phase planes for System (3) when the values of \(\frac{\sigma^2_K}{\sigma^2_u}\) are small enough. The red dots denote the equilibria \((x^*, u^*)\) are sources, the green dots denote the equilibria are saddle nodes, and the blue dots denote the equilibria are stable nodes.

(b) **Intermediate values of** \(\frac{\sigma^2_K}{\sigma^2_u}\): Numerical simulations suggest that the intermediate values of \(\frac{\sigma^2_K}{\sigma^2_u}\) tend to generate multiple ESS. In this case, there are two pairs of symmetric interior equilibria \((x^*, \pm u^*)\) with one pair as saddles and the other as sinks.

i. If \(r > a_0\), then both pairs are the interior carrying capacity equilibria (see Figure 4(a)-4(b) for the dynamical structure of this case).

ii. If \(r < a_0\), then either one pair forms the interior Allee threshold, while the other is the interior carrying capacity equilibria; or both pairs are the interior carrying capacity equilibria. In addition, we observe that the boundary Allee threshold \((x^K(0), 0)\) is a source (see Figure 4(c) for the dynamical structure of this case).

(c) **Large values of** \(\frac{\sigma^2_K}{\sigma^2_u}\): According to Proposition 3.1 and Theorem 3.1, we know that Model (3) can have interior equilibrium \((x^*, \pm u^*)\) and the boundary carrying capacity equilibrium \((x^K(0), 0)\) is a saddle. In the case that the inequalities \(\frac{4}{hK} < r < a\) hold or the following inequalities hold

\[
\max\{r, \frac{1}{hK}\} < a < \sqrt{\frac{r}{K}} \left(\frac{2 + \sqrt{r}hK}{4 - rhK}\right) \text{ and } r < \frac{4}{hK},
\]


(a) Schematic phase plane for System (3) having three ESS when $r < a_0$

(b) Basins of attractions for three ESS of System (3) when $r < a_0$

(c) Schematic phase plane for System (3) having three ESS when $r > a_0$

Figure 4: The intermediate values of $\sigma^2 K_a$. In Figure 4(a)-4(c), the red dots denote the equilibria $(x^*, u^*)$ are sources, the green dots denote the equilibria are saddle nodes, and the blue dots denote the equilibria are stable nodes. In Figure 4(b), the red region is the basin attraction for $(x^K(0), 0)$, the green region is the basin attraction for $(x^K(-u^K), -u^K)$, and the blue region is the basin attraction for $(x^K(u^K), u^K)$.

Then the boundary Allee threshold $(x^d(0), 0)$ exists and it is a source. For both $r > a_0$ and $r < a_0$, simulations suggest that there exists stable interior carrying capacity equilibrium $(x^K(u^K), u^K)$ which are also ESS (see Figure 5 for the dynamical structure of Model (3) when the values of $\sigma^2 K_a$ are large).

5. Discussion

Allee effects, positive correlations between the per capita growth rate and population densities/sizes at low population densities/sizes, play an important role in investigations of endangered species, invasive species, and epidemiology (Keitt and Holt 2001; Kramer et al 2009; Thieme et al 2009; Kang and Castillo-Chavez b&c). There is a rapidly growing interest in studying the impacts of Allee effects in ecological dynamics such as competitive systems, predator-prey interactions, food-webs and also in evolutionary dynamics. In this manuscript, we applied the framework of evolutionary game theory (EGT) with continuous strategy dynamics to study the evolutionary outcomes of a single species subject to Allee effects induced by mating limitations or predation satiation.
Our study of the Allee effect EGT model indicates that the maximum per capita growth rate \( r \) the population carrying capacity \( K(u) \) and the anti-predation ability \( a(u) \) play important roles in evolutionary outcomes. Here, we assume that both \( K(u) \) and \( a(u) \) are Gaussian distributed around mean trait \( u = 0 \) with variances \( \sigma^2_{K}, \sigma^2_{a} \), respectively. These distributions assume the maximum inherent equilibrium level \( K_0 \) and the minimum anti-predation for species using strategy \( u \) are attained at trait boundary \( u = 0 \), i.e., \( K(u) = K_0 e^{-\frac{u^2}{2\sigma^2_{K}}} \) and \( a(u) = a_0 e^{-\frac{u^2}{2\sigma^2_{a}}} \), which creates a trade-off between prey carrying capacity and anti-predation abilities.

The fitness of our investigated species can be defined as the ratio of its carrying capacity and the anti-predation ability: \( \frac{K(u)}{a(u)} = \frac{K_0 e^{-\frac{u^2}{2\sigma^2_{K}}}}{a_0 e^{-\frac{u^2}{2\sigma^2_{a}}}} \left[ 1 - \frac{u^2}{\frac{K^2}{\sigma^2_{K}}} \right] \) which is influenced by the values of the \( \Delta_{Ka} = \frac{\sigma^2_{K}}{\sigma^2_{a}} \). Notice that larger values of \( \Delta_{Ka} \) produce greater fitness value. One rationale for this is that \( \Delta_{Ka} \) capture the extent of the biological trade-off between trait investments in predator evasion versus competitive ability. Large values of \( \Delta_{Ka} \) suggest a relative small tradeoff because here, the species can exhibit extreme trait values for anti-predation (i.e. \( |u| >> 0 \)) without affecting their carrying capacity. Similarly, small values of \( \Delta_{Ka} \) suggest a relative large tradeoff because there are only relatively small changes in anti-predation ability away from the trait boundary (i.e. \( u = 0 \)). These observations are consistent with our analytical results in Section 5 on the impacts of \( \Delta_{Ka} \) on the global model dynamics:

1. With the large values of \( \Delta_{Ka} \), the evolutionary model tends to have a pair of symmetric interior carrying capacity interior ESS equilibrium \( (x^K(u^K), u^K) \) which are not strong Allee effects equilibria, even when its ecological system has the boundary strong Allee effect equilibrium \( (x^K(0), 0) \). This suggests that evolution may suppress strong Allee effects when the values of \( \Delta_{Ka} \) are large.

2. With the small values of \( \Delta_{Ka} \), the evolutionary model only has the boundary carrying capacity ESS equilibrium \( (x^K(0), 0) \) when its ecological dynamics has no Allee effect. However, the evolutionary model tends to have multiple ESS (i.e., the boundary carrying capacity ESS equilibrium \( (x^K(0), 0) \) and the interior carrying capacity equilibrium \( (x^K(u^K), u^K) \)) when its ecological dynamics has the boundary strong Allee effect equilibrium. In the latter case, the interior carrying capacity equilibrium ESS tends to have small population density which may potentially serve as an Allee threshold since demographic stochasticity can drive species to extinction. This suggests that evolution may preserve strong Allee effects if not suppress strong Allee effects when the values of \( \Delta_{Ka} \) are small enough by creating a potential Allee threshold.

3. With the intermediate values of \( \Delta_{Ka} \), the evolutionary model tends to have multiple ESS equilibrium regardless of whether its ecological dynamics has strong Allee effects or not. One consequence of this is that when the initial state \((x(0), u(0))\) lies near the boundary of the basins of attraction,
chance perturbation that reduce population size and/or phenotypic variance (e.g. drought, invading predators, etc.) may drive the prey species to different ESS equilibria (see Figure 4(b) for a numerical example).

Thus, we conclude that (a) Evolution may suppress strong Allee effects when the values of $\Delta_{K_a}$ are large while evolution may preserve strong Allee effects when the values of $\Delta_{K_a}$ are small enough by generating a low population density ESS equilibrium served as potential Allee threshold; and (b) The intermediate values of $\Delta_{K_a}$ are causes for multiple evolutionary stable strategies (ESS) of our component Allee effect EGT model. This conclusion addresses the first two questions proposed in the introduction.

There are a number of ecological studies (e.g., see Strobe et al. 2011; O’steen et al. 2002; McPeek 1997; Fitzgibbon 1994, etc) support our assumptions about growth/predation risk trade-offs and predator-induced trait evolution. O’steen et al. (2002) provide empirical evidences of a negative correlation between anti-predation phenotypes with competitive ability in group-living Trinidadian Guppies (Poecilia Reticula). They show convincingly that changes in predation pressures (i.e. in high risk vs. low risk environments) favors evolutionary changes in the predator evasion strategies over fairly short generational times (15-20 years). More importantly, their results along with others (Reznick et al. 2001) suggest such investments can carry heavy fitness costs. This provides some biological rationale for Proposition 4.3, namely, that evolutionary extinction can occur if minimizing anti-predation risk yields insufficient increases to the species per-capita growth rate.

The possibility of multiple ESSs highlights the path dependence of our model and carries important biological implications. A catastrophic reduction in prey density (e.g. due to famine, disease, etc) might push the population into regions where selection favors phenotypes that weaken or strengthen Allee effects. In the latter case, the presence of an Allee threshold increases the likelihood of further population declines which may result in stochastic extinctions. Previous work by Kramer et al. (2009) and Gascoigne and Lipcius (2004) documented evidence of predator-driven strong Allee effects in endangered populations like the Australian Kangaroo rat (Quokka Setonix brachyurus) and Hutton’s shearwater (Puffinus huttoni). In both species, attempts at reintroduction have been fraught with setbacks linked primarily to mate-finding limitations and predation. Our results highlight the importance of careful design and implementation of species restoration efforts that weigh the potential selection pressures and the contexts of ecological interactions affecting the probability of successful re-establishment. These considerations are even more pertinent in the face of mounting evidence that trait evolution can occur on fast enough to affect ecological interactions (e.g., see Kinnison and Hairston 2007).

Another interesting finding of our study is that the values of the maximum per capita growth rate $r$ and the distribution of anti-predation in traits $a(u)$ play critical roles in determining whether the extinction equilibrium $(0,u^*)$ is an ESS attractor; while the carrying capacity $K(u)$ has no such effects. For our evolutionary model, we assume that the anti-predation ability $a(u)$ follows a Gaussian distribution in its phenotypic trait $u$ with variances $\sigma_a^2$. This assumption contributes to the fact that trait evolution can prevent species extinction even when the population has strong Allee effects. However, this conclusion does not hold if $a'(u^*) = 0$, $a''(u^*) > 0$ and $r < a(u^*) \leq \max_{v \in \mathbb{R}} \{a(v)\}$ is satisfied as noted in Proposition 4.3. This result addresses our last last question regarding the potential mechanisms that contribute to the emergence of an EES extinction equilibrium.

6. Proofs

Proof of Lemma 2.1

Proof. Items 1 and 2 in Lemma 2.1 can be obtained through straight forward calculations, thus we focus on showing item 3. In order to have $x^\theta, x^K$ being positive, the following conditions have to be satisfied:

$x^\theta + x^K = \frac{haK - 1}{ha} > 0$, $x^\theta x^K = \frac{K(a - r)}{ahr} > 0$ and $r \left|1 + haK\right|^2 > 4ha^2K$
where the last inequality indicates that $r[1+haK]^2 > 4ha^2K$ holds if $rhK > 4$ or $rhK < 4$ and $a < \sqrt{\frac{4}{khK}} \left(\frac{2 + \sqrt{7hK}}{2 - rhK}\right)$. Therefore, we can conclude that Model (1) has equilibria $x^0$ and $x^K$ if either $a > r > \frac{1}{aK} \max\{r, \frac{1}{rhK}\}$ or $a < \sqrt{\frac{4}{khK}} \left(\frac{2 + \sqrt{7hK}}{2 - rhK}\right)$ and $r < \frac{4}{hK}$ hold. The local stability of $x^0, x^*, x^K$ is determined by the sign of $F'(x) = H(x) + xH'(x) = H(x) + x \left[-a + \frac{a^2h}{(ha + 1)^2}\right]$. This indicates that $F'(x^0) = H(0) = r - a < 0$ and thus $x^0 = 0$ is locally asymptotically stable. Notice that $F(x)$ and also be rewritten as $F(x) = \frac{rx(x-x^0)(x^K-x)}{hax+1}$. Therefore, we have

\[
F'(x^0) = \frac{rx^0(x^K-x^0)}{hax^0+1} > 0 \quad \text{and} \quad F'(x^K) = -\frac{rx^K(x^K-x^0)}{hax^K+1} < 0
\]

which implies that $x^0$ is always a saddle and $x^K$ is always locally asymptotically stable.

In the case that $r[1+haK]^2 < 4ha^2K$ (i.e., $a > \sqrt{\frac{4}{khK}} \left(\frac{2 + \sqrt{7hK}}{2 - rhK}\right) > 0$), then both $x^0$ and $x^K$ are complex. Thus, if $a > \max\{\sqrt{\frac{4}{khK}} \left(\frac{2 + \sqrt{7hK}}{2 - rhK}\right), \frac{1}{hK}, r\}$ and $rhK < 4$, then Model (1) has only extinction equilibrium $x^0 = 0$ which is locally asymptotically stable.

\[\square\]

\textit{Proof of Proposition 3.1}

\textit{Proof.} An equilibrium $(x^*, u^*)$ of the evolutionary model (3) requires

\[
x^*H(x^*, u^*) = 0 \quad \text{and} \quad \sigma^2 u^* \left[\frac{r x^*}{\sigma_K^2 K(u^*)} + \frac{a(u^*)}{\sigma^2(1 + ha(u^*)x^*)^2}\right] = 0
\]

which gives $x^* = x^0 = 0$ or $x^* = \frac{[ha(u^*)K(u^*)-1]+\sqrt{[ha(u^*)K(u^*)-1]^2+4ha(u^*)K(u^*)[1-a(u^*)]}}{2ha(u^*)}$ and

\[
u^* = 0 \quad \text{or} \quad \frac{r x^*}{\sigma_K^2 K(u^*)} + \frac{a(u^*)}{\sigma^2(1 + ha(u^*)x^*)^2} = 0.
\]

If $u^* = 0$, then $a(0) = a_0$ and $K(0) = K_0$. Thus, according to Lemma 2.1, the evolutionary model of a single species with a component Allee effect induced by predator satiation (3) has the following properties:

- If $a_0 < r$, then the evolutionary model (3) can have the following two equilibria:

\[(0, 0) \quad \text{and} \quad (x^K(0), 0) = \left(\frac{[ha_0 K_0 - 1] + \sqrt{[ha_0 K_0 - 1]^2 + 4ha_0 K_0 \left[1 - \frac{a_0}{2r}\right]}}{2ha_0}, 0\right)
\]

- If $\frac{1}{a_0 hK_0} < r < a_0$ hold or the following inequalities hold

\[\max\{r, \frac{1}{a_0 hK_0}\} < a < \sqrt{\frac{r}{K_0 h} \left(\frac{2 + \sqrt{7hK_0}}{4 - rhK_0}\right)} \quad \text{and} \quad r < \frac{4}{hK_0},
\]

then the evolutionary model (3) can have the following three equilibria: $(0, 0)$,

\[(x^0(0), 0) = \left(\frac{[ha_0 K_0 - 1] - \sqrt{[ha_0 K_0 - 1]^2 + 4ha_0 K_0 \left[1 - \frac{a_0}{2r}\right]}}{2ha_0}, 0\right)
\]

and

\[(x^K(0), 0) = \left(\frac{[ha_0 K_0 - 1] + \sqrt{[ha_0 K_0 - 1]^2 + 4ha_0 K_0 \left[1 - \frac{a_0}{2r}\right]}}{2ha_0}, 0\right).
\]
Therefore, we have the following two scenarios:

\[
 r \left(1 - \frac{x^*}{K(u^*)}\right) = \frac{a(u^*)}{1 + 4a(u^*)x^*}; \quad \frac{r x^*}{\sigma K(u^*)} = \frac{a(u^*)}{\sigma^2(1 + 4a(u^*)x^*)}. 
\]

Therefore, \( x^* = f(a(u^*)) = \frac{1}{2r K} - \frac{1}{h a(u^*)} + \frac{\sqrt{1 + 4r \frac{\sigma K}{a(u^*)}}}{{2r h}} \). By simple calculations, we are able to show that the positivity of \( f(a(u^*)) \) requires \( r < a(u^*) [1 + (\frac{2K}{\sigma})^2] \). Therefore, Model (3) has no interior equilibrium \((x^*, u^*)\) if \( a(u^*) = a_0 e^{-\frac{(u^*)^2}{2\sigma^2}} < a_0 < \frac{r}{1 + (\frac{2K}{\sigma})^2} \). In addition, we have

\[
 K(u^*) = \frac{\sigma a f(a(u^*)) \left[ 1 + \sqrt{1 + 4r \frac{\sigma K}{a(u^*)}} \right]^2}{4r^2 h \sigma^2 K} = \phi(a(u^*)) \tag{10}
\]

by replacing \( f(a(u^*)) \) with \( \frac{1}{2r h} - \frac{1}{h a(u^*)} + \frac{\sqrt{1 + 4r \frac{\sigma K}{a(u^*)}}}{{2r h}} \) in the term \( \frac{1}{1 - \frac{1}{4r h a(u^*)} \phi(a(u^*))} \).

Alternatively, we can also obtain the same expression (10) by letting

\[
f(a(u^*)) = x^\theta(u^*) \text{ or } f(a(u^*)) = x^K(u^*).
\]

Note that \( \lim_{u \to \infty} K(u) = 0 \) and \( \lim_{u \to -\infty} f(a(u)) = -\infty \Rightarrow \lim_{u \to \infty} \phi(a(u)) = -\infty \), thus there is at least one \( u > 0 \) such that (10) holds if the following inequalities hold

\[
 K(0) = K_0 < \phi(a(u)) |_{u=0} = \phi(a_0) = \frac{\sigma a \left[ \frac{1}{2r h} - \frac{1}{h a_0} + \frac{\sqrt{1 + 4r \frac{\sigma K}{a_0 \sigma^2}}}{{2r h}} \right] \left[ 1 + \sqrt{1 + 4r \frac{\sigma K}{a_0 \sigma^2}} \right]^2}{4r^2 h \sigma^2 K}. \tag{11}
\]

Therefore, Model (3) has at least one interior equilibrium \((x^*, u^*)\) with \( x^* u^* > 0 \) if (11) holds. \(\square\)

**Proof of Theorem 3.1**

**Proof.** The earlier discussion covers the existence requirement for the equilibrium of the single species evolutionary model (3), thus we only focus on sufficient conditions that lead to the equilibrium being a sink, or a saddle, or a source. For convenience, let \( a^* = a(u^*) \), \( f^* = f(a(u^*)) \) and \( K^* = K(u^*) \).

Notice that \( \frac{\partial G(v, u, x)}{\partial v} = 0 $$, \( \frac{\partial G(v, u, x)}{\partial u} = 0 $$, and \( \frac{\partial^2 G(v, u, x)}{\partial v \partial u} = 0 $$ for Model (3), thus the local stability of the equilibrium \((x^*, u^*)\) is determined by its Jacobian matrix (12) evaluated at \((x^*, u^*)\):

\[
 J(x^*, u^*) = \begin{bmatrix}
 x^* \frac{\partial G(u^*, u^*, x^*)}{\partial x} & 0 \\
 \frac{\sigma}{\sigma^2} \frac{\partial^2 G(u^*, u^*, x^*)}{\partial v \partial x} & \sigma^2 \frac{\partial^2 G(u^*, u^*, x^*)}{\partial v^2}
\end{bmatrix} 
\]

whose eigenvalues are

\[
 \lambda_1(x^*, u^*) = \sigma^2 \left[ -\frac{r x^*}{\sigma^2 K^*} + \frac{a^*}{\sigma^2 (1 + 4a(u^*)x^*)} \right] + \sigma^2 (u^*)^2 \left[ -\frac{r x^*}{\sigma^2 K^*} + \frac{a^*(ha^* x^* - 1)}{\sigma^2 (1 + 4a(u^*)x^*)} \right]. 
\]

\[
 \lambda_2(x^*, u^*) = x^* \left[ -\frac{r}{K^*} + \frac{b(a^*)^2}{(1 + 4a(u^*)x^*)^2} \right] + \left[ r(1 - \frac{x^*}{K^*}) - \frac{a^*}{1 + 4a(u^*)x^*} \right]. 
\]

Therefore, we have the following two scenarios:

1. If \( u^* = 0 \), we have the following three cases:

   (a) The trivial equilibrium \((0, 0)\) is always unstable since \( \lambda_1(0, 0) = \frac{\sigma^2 a_0}{\sigma^2} > 0 \) and \( \lambda_2(0, 0) = r - a_0 \).

   Moreover, \((0, 0)\) is a saddle if \( r < a_0 \) and it is a source if \( r > a_0 \).
(b) According to Lemma 2.1, the equilibrium \((x^\theta(0),0)\) exists and is always unstable if \(\frac{a}{h_{K_{0}}} < r < a_{0}\) or \(\max\{r, \frac{1}{h_{K_{0}}}\} < a_{0} \sqrt{\frac{2}{\lambda_{0}} \left( \frac{2 + \sqrt{h_{K_{0}}}}{4 - rh_{K_{0}}} \right) }\) and \(r < \frac{4}{h_{K_{0}}} \). Thus, we have \(\lambda_{2}(x^{\theta}(0),0) = x^{\theta}(0) \left[ -\frac{r}{K_{0}} + \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))} \right] > 0 \Leftrightarrow \frac{r}{K_{0}} < \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))}\) while the other eigenvalue \(\lambda_{1}(x^{\theta}(0),0) = \sigma_{2}^{\theta} \left[ -\frac{r_{x^{\theta}(0)}}{\sigma_{K}^{2}K_{0}} + \frac{a_{0}}{\sigma_{2}^{\theta}(1 + h_{a}x^{\theta}(0))} \right] \) can be positive or negative. If the equality \(h_{a \theta}(0) = \sigma_{2}^{\theta} \) holds, then we have \(\frac{r_{x^{\theta}(0)}}{\sigma_{K}^{2}K_{0}} < \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))} < \frac{a_{0}}{\sigma_{2}^{\theta}(1 + h_{a}x^{\theta}(0))}\) which indicates that \((x^{\theta}(0),0)\) is a source.

(c) From Lemma 2.1, we know that \(x^{K}(0)\) is ESE whenever it exists. This implies that whenever \([r > a_{0} or [\frac{4}{h_{K_{0}}} < r < a_{0}] or [\max\{r, \frac{1}{h_{K_{0}}}\} < a_{0} \sqrt{\frac{2}{\lambda_{0}} \left( \frac{2 + \sqrt{h_{K_{0}}}}{4 - rh_{K_{0}}} \right) }\) and \(r < \frac{4}{h_{K_{0}}} \) hold, we always have \(\lambda_{2}(x^{K}(0),0) = -\frac{r}{K_{0}} + \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(0))} < 0 \Leftrightarrow \frac{r}{K_{0}} > \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(0))}\) which gives \(\frac{r_{x^{K}(0)}}{\sigma_{K}^{2}K_{0}} > \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(0))}\). Notice that \(\lambda_{1}(x^{K}(0),0) = \sigma_{2}^{2} \left[ -\frac{r_{x^{K}(0)}}{\sigma_{K}^{2}K_{0}} + \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}x^{K}(0))} \right] \), therefore, \((x^{K}(0),0)\) is locally asymptotically stable if the equality \(h_{a \theta}(0) > \sigma_{2}^{2} \) holds since \(\frac{r_{x^{K}(0)}}{\sigma_{K}^{2}K_{0}} > \frac{h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(0))} > \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}x^{K}(0))}\). Thus, we can conclude that \((x^{K}(0),0)\) is locally asymptotically stable if \(\frac{r_{x^{K}(0)}}{\sigma_{K}^{2}K_{0}} < h_{a \theta}(0)\).

If \(\frac{4}{h_{K_{0}}} < r < a_{0}\) or \(\max\{r, \frac{1}{h_{K_{0}}}\} < a_{0} \sqrt{\frac{2}{\lambda_{0}} \left( \frac{2 + \sqrt{h_{K_{0}}}}{4 - rh_{K_{0}}} \right) }\) and \(r < \frac{4}{h_{K_{0}}} \) hold, then Model (3) has two boundary equilibria \((x^{\theta}(0),0)\) and \((x^{K}(0),0)\) and the following inequalities hold

\[
\frac{h(a)^2}{(1 + h_{a}x^{K}(0))} < \frac{r}{K_{0}} < \frac{h(a)^2}{(1 + h_{a}x^{\theta}(0))},
\]

which is equivalent to

\[
\frac{x^{\theta}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))} < \frac{r_{x^{\theta}(0)}}{\sigma_{K}^{2}K_{0}} < \frac{x^{K}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(0))},
\]

\[x^{*} = x^{\theta}(0), x^{K}(0)\). Therefore, if in addition, the inequalities \(h_{a \theta}(0) < \sigma_{2}^{2} \) hold, then we can conclude that \((x^{\theta}(0),0)\) is a source and \((x^{K}(0),0)\) is a sink. However, if \(\frac{x^{\theta}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))} > \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}x^{\theta}(0))}\) holds, then we have \(\frac{r_{x^{\theta}(0)}}{\sigma_{K}^{2}K_{0}} > \frac{x^{\theta}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{\theta}(0))} > \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}x^{\theta}(0))}\) which implies that \((x^{\theta}(0),0)\) is a saddle. Similarly, if \(\frac{x^{K}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}(x^{K}(0)))} < \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}(x^{K}(0)))}\) holds, then we have \(\frac{r_{x^{K}(0)}}{\sigma_{K}^{2}K_{0}} < \frac{x^{K}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}(x^{K}(0)))} < \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}(x^{K}(0)))}\). Thus, we can conclude that \((x^{K}(0),0)\) is a saddle if \(\frac{x^{K}(0)h(a)^2}{\sigma_{K}^{2}(1 + h_{a}(x^{K}(0)))} < \frac{a_{0}}{\sigma_{2}^{2}(1 + h_{a}(x^{K}(0)))}\).

2. If \(u^{*} \neq 0\), then \(x^{*}u^{*} \neq 0\). In this case, we have \((x^{*}, u^{*}) = (x^{\theta}(u^{*}), u^{\theta})\) or \((x^{*}, u^{*}) = (x^{K}(u^{*}), u^{K})\). According to Lemma 2.1, we know that \(x^{\theta}(u^{*})\) is always unstable while \(x^{K}(u^{*})\) is always locally asymptotically stable for the ecological model (1), i.e., the second eigenvalue \(\lambda_{2}(x^{\theta}(u^{*}), u^{ \theta}) > 0\) and \(\lambda_{2}(x^{K}(u^{*}), u^{K}) < 0\) which gives \(\frac{r_{x^{K}}}{\sigma_{K}^{2}} < \frac{x^{K}(u^{*})h(a)^2}{\sigma_{K}^{2}(1 + h_{a}x^{K}(u^{*}))}\). Therefore, assume the existence of the equilibrium \((x^{\theta}(u^{*}), u^{\theta})\) and \((x^{K}(u^{*}), u^{K})\), then the equilibrium \((x^{\theta}(u^{*}), u^{\theta})\) is always unstable for the evolutionary model (3) while \((x^{K}(u^{*}), u^{K})\) can be locally asymptotically stable if, in addition, the following condition holds

\[
\lambda_{1}(x^{K}(u^{K}), u^{K}) = \sigma_{2}^{2}(u^{K})^{2} \left[ \frac{r_{x^{K}}}{\sigma_{K}^{2}K^{*}} + \frac{a^{*} (ha^{*}x^{K} - 1)}{\sigma_{2}^{2}(1 + h_{a}x^{K})^{3}} \right] < 0 \Leftrightarrow \frac{r_{x^{K}}}{\sigma_{K}^{2}K^{*}} > \frac{a^{*} (ha^{*}x^{K} - 1)}{\sigma_{2}^{2}(1 + h_{a}x^{K})^{3}} \tag{14}
\]

where \(x^{K} = x^{K}(u^{K}), a^{*} = a(u^{K})\) and \(K^{*} = K(u^{K})\).

Since \((x^{K}(u^{K}), u^{K})\) is an equilibrium of Model (3), thus we have the following equality (15)

\[
\frac{r_{x^{K}}}{\sigma_{K}^{2}K^{*}} = \frac{a^{*}}{\sigma_{2}^{2}(1 + h_{a}x^{K})^{2}} \Leftrightarrow \frac{r_{x^{K}}}{\sigma_{K}^{2}K^{*}} = \frac{a^{*}}{\sigma_{2}^{2}\sigma_{K}^{2}(1 + h_{a}x^{K})^{2}}. \tag{15}
\]
Therefore, either one of the following two inequalities is a sufficient condition that guarantees the inequality (14)

\[
\frac{rx^K}{\sigma_K K^*} = \frac{a^*}{\sigma_a^2 \sigma_K^2 [1 + ha^*x^K]^2} > \frac{a^* (ha^*x^K - 1)}{\sigma_a^2 (1 + ha^*x^K)^3}
\] (16)

or

\[
\frac{rx^K}{\sigma_K K^*} > \frac{x^K h(a^*)^2}{\sigma_K^2 (1 + ha^*x^K)^2} > \frac{a^* (ha^*x^K - 1)}{\sigma_a^2 (1 + ha^*x^K)^3}.
\] (17)

The inequality (16) is equivalent to

\[
\frac{\sigma_a^2}{\sigma_K^2} > \frac{ha^*x^K - 1}{1 + ha^*x^K} \Leftrightarrow \frac{\sigma_a^2}{\sigma_K^2} < \frac{1 + ha^*x^K}{ha^*x^K - 1}.
\] (18)

While the inequality (17) can be guaranteed by

\[
\left(\frac{\sigma_a^2}{\sigma_K^2}\right)^2 < \frac{a^*hx^K(1 + ha^*x^K)}{ha^*x^K - 1}.
\] (19)

From Proposition 3.1, we know that Condition (11) and \(K^* < 2f(a^*) + \frac{1}{ha^*}\) can guarantee the existence of the interior equilibrium point \((x^K(u^K), u^K)\), and either Condition (18) or Condition (19) can guarantee \((x^K(u^K), u^K)\) being locally asymptotically stable. Similarly, we are able to show that if the following inequalities (20) hold

\[
\frac{rx^K}{\sigma_K K^*} = \frac{a^*}{\sigma_a^2 \sigma_K^2 [1 + ha^*x^K]^2} < \frac{a^* (ha^*x^K - 1)}{\sigma_a^2 (1 + ha^*x^K)^3} \Leftrightarrow \frac{\sigma_a^2}{\sigma_K^2} < \frac{ha^*x^K - 1}{1 + ha^*x^K} \Leftrightarrow \frac{\sigma_a^2}{\sigma_K^2} > \frac{1 + ha^*x^K}{ha^*x^K - 1},
\] (20)

then \((x^K(u^K), u^K)\) is a saddle.

Similarly, we are able to show that Condition (11) and \(K^* > 2f(a^*) + \frac{1}{ha^*}\) can guarantee the existence of the interior equilibrium point \((x^\theta(u^\theta), u^\theta)\), and the following additional condition (21)

\[
\frac{\sigma_a^2}{\sigma_K^2} < \min\left\{\frac{ha^*x^\theta - 1}{1 + ha^*x^\theta}, \sqrt[4]{\frac{ha^*x^\theta - 1}{a^*ha^\theta(1 + ha^*x^\theta)}}\right\} \Leftrightarrow \min\left\{\frac{1 + ha^*x^\theta}{ha^*x^\theta - 1}, \sqrt[4]{\frac{a^*ha^\theta(1 + ha^*x^\theta)}{ha^*x^\theta - 1}}\right\}
\] (21)

can guarantee \((x^\theta(u^\theta), u^\theta)\) being a source; while \((x^\theta(u^\theta), u^\theta)\) is a saddle if the following additional condition (22)

\[
\frac{\sigma_a^2}{\sigma_K^2} > \frac{ha^*x^\theta - 1}{1 + ha^*x^\theta} \Leftrightarrow \frac{\sigma_a^2}{\sigma_K^2} < \frac{1 + ha^*x^\theta}{ha^*x^\theta - 1}.
\] (22)

For convenience, the existence and stability conditions of the equilibrium of the evolutionary model (3) are listed in Table 1.

\[\square\]

**Proof of Theorem 3.2**

**Proof.** Recall that an ESS of Model (3) requires the equilibrium \((x^*, u^*)\) is a locally asymptotically stable. Thus according to Theorem 3.1, the potential candidate for ESS are \((x^K(0), 0)\) and \((x^K(u^K), u^K)\).

Assume that \((x^K(0), 0)\) is locally asymptotically stable, then it is an ESS if it satisfies ESS maximum principle (23), i.e.,

\[
\max_{v \in \mathbb{R}} \{G(v, 0, x^K(0))\} = G(0, 0, x^K(0)) = 0.
\] (23)
Note that \( G(v, 0, x^K(0)) = r \left( 1 - \frac{x^K(0)}{K(v)} \right) - \frac{a(v)}{1 + ha(v)x^K(0)} \) is an even function of \( v \) and \( G(0, 0, x^K(0)) = 0 \), thus the ESS maximum principle (23) holds if the following inequality holds

\[
\frac{\partial G(v, 0, x^K(0))}{\partial v} = v \left[ -\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^K(0))^2} \right] \leq 0 \text{ for } v \geq 0. \tag{24}
\]

Notice that \(-\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 K(v)} \leq -\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 K(v)} \leq -\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^K(0))^2} \), thus either \(-\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 K(v)} \leq 0 \) or \(sup_{v>0} \left\{ -\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^K(0))^2} \right\} \leq 0 \). 

Since \( r_x^2 \sigma^2_{\sigma^2} \leq \frac{1}{\sigma^2_{\sigma^2}} - \frac{1}{\sigma^2_{\sigma^2}} \) we have \( -\frac{rx^K(0)}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 K(v)} \leq 0 \) and \( \frac{a(v)}{\sigma_K^2 K(v)} \leq -\frac{rx^K(0)}{\sigma_K^2 K(v)} \) can guarantee (24). The latter case comes from the fact that \( G(v, 0, x^K(0)) \) satisfies the ESS maximum principle if \( \frac{a(v)}{\sigma_K^2 K(v)} \leq -\frac{rx^K(0)}{\sigma_K^2 K(v)} \) or \( \frac{a(v)}{\sigma_K^2 K(v)} \leq \frac{1}{\sigma^2_{\sigma^2}} \). Combined with sufficient conditions that guarantee \( (x^K(0), 0) \) being locally asymptotically stable from Theorem 3.1, we can conclude that if \( r > a_0 \), or \( \frac{4}{r} < a_0 \) holds, then the boundary carrying capacity equilibrium \( (x^K(0), 0) \) is an ESS if, in addition, either \( \frac{a(v)}{\sigma^2_{\sigma^2}} \leq \min \left\{ \frac{r x^K(0)}{a_0 K_0}, \frac{a(v)}{\sigma^2_{\sigma^2}} \right\} \) or \( \frac{a(v)}{\sigma^2_{\sigma^2}} \leq \min \left\{ \frac{r x^K(0)}{a_0 K_0}, \frac{a(v)}{\sigma^2_{\sigma^2}} \right\} \) holds.

Therefore, the statement is true.

\( \square \)

**Proof of Theorem 3.3**

Proof. According to Proposition 3.1 and Theorem 3.1, if the inequality \( \frac{\sigma^2_{\sigma^2}}{\sigma^2_{\sigma^2}} < \frac{r}{a_0} - 1 \) holds, then Model (3) has only two equilibria \((0,0)\) and \((x^K(0),0)\), where \((0,0)\) is a saddle. From the proof of Theorem 3.1, we know that the boundary carrying capacity equilibrium \((x^K(0),0)\) is locally asymptotically stable if \( \lambda_1(x^K(0),0) = \sigma^2_{\sigma^2} \left[ -\frac{r x^K(0)}{K_0} + \frac{a(v)}{\sigma^2_{\sigma^2} (1 + ha_0 x^K(0))^2} \right] < 0 \) which is equivalent to \( \frac{\sigma^2_{\sigma^2}}{\sigma^2_{\sigma^2}} < \frac{r x^K(0)}{a_0 K_0} \). Notice that \( r \left( 1 - \frac{x^K(0)}{K_0} \right) = \frac{a(v)}{1 + ha_0 x^K(0)} \Leftrightarrow \frac{a(v)}{r} = \left( 1 + ha_0 x^K(0) \right) \left( 1 - \frac{x^K(0)}{K_0} \right) \), thus we have

\[
\frac{r x^K(0)}{a_0 K_0} - \frac{a(v)}{r} + 1 = \frac{a(v)}{r} \left( 1 + ha_0 x^K(0) \right) \left( 1 + \frac{ha_0 x^K(0)}{K_0} \right) - 1 > 0
\]

which implies that \( a_0 - 1 < \frac{r x^K(0)}{a_0 K_0} \). Therefore, we have \( \sigma^2_{\sigma^2} < \frac{r}{a_0} - 1 < \frac{r x^K(0)}{a_0 K_0} \) which indicates that \((x^K(0),0)\) is locally asymptotically stable.

On the other hand, we have \( x^K(0) < K_0 \) and the following inequalities

\[
\frac{r x^K(0)}{a_0 K_0} - \frac{a(v)}{r} + 1 = \frac{a(v)}{r} \left( 1 + ha_0 x^K(0) \right) > 0 .
\]

Therefore, we have \( \sigma^2_{\sigma^2} < \frac{r}{a_0} - 1 < \frac{r x^K(0)}{a_0 K_0} \) which indicates that \((x^K(0),0)\) satisfies the ESS maximum principle according to Theorem 3.2. Therefore, the boundary carrying capacity equilibrium \((x^K(0),0)\) has convergence stability (i.e., it is locally asymptotically stable) and satisfies ESS maximum principle, i.e., it is ESS.

\( \square \)
Proof of Theorem 3.4
Proof. Since the interior carrying capacity \((x^*, u^*) = (x^K(u^K), u^K)\) is locally asymptotically stable, then it is an ESS if it satisfies the ESS maximum principle, i.e.,

\[
\max_{v \in \mathbb{R}} \{G(v, u^*, x^*)\} = G(u^*, u^*, x^*) = 0. \tag{25}
\]

Since \(G(v, u^*, x^K(u^*))\) is an even function of \(v\) and \(G(u^*, u^*, x^*) = 0\), then if the following conditions hold

\[
\frac{\partial G(v, u^*, x^*)}{\partial v} = v \left[ \frac{-r x^*}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^*)^2} \right] \leq 0 \text{ for } v \geq u^* \tag{26}
\]

\[
\frac{\partial G(v, u^*, x^*)}{\partial v} = v \left[ -\frac{r x^*}{\sigma_K^2 K(v)} + \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^*)^2} \right] \geq 0 \text{ for } 0 < v \leq u^*, \tag{27}
\]

we can conclude that the ESS maximum principle (25) holds. According to the proof of Theorem 3.2, we know that either \(\frac{\sigma_k^2}{\sigma_a} \leq \frac{r x^*}{\sigma_K^2 K(v)}\) or \(\frac{\sigma_k^2}{\sigma_a} \leq \max \{ 1, \frac{r a h^2 (x^*)^2}{K_h} \}\) can guarantee that (26) holds.

If \(0 < v \leq u^*\), then we have \(\frac{\partial G}{\partial v} \leq \frac{r x^*}{\sigma_K^2 K(v)} = \frac{a(u^*)}{\sigma_K^2 (1 + ha(u^*)x^*)^2} \). Let \(k(v) = \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^*)^2}\), then we have \(k'(v) = -\frac{a(u^*)}{\sigma_K^2 (1 + ha(u^*)x^*)^2}(1 - 2a(v)hx^*)\). Since \(a'(v) < 0\) for \(v > 0\), thus if \(x^* < \frac{1}{2a(v)h} < \frac{1}{2a(0)h}\), then we have \(k'(v) < 0\) for \(v > 0\) and \(\frac{a(u^*)}{\sigma_K^2 (1 + ha(u^*)x^*)^2} < \frac{a(v)}{\sigma_K^2 (1 + ha(v)x^*)^2}\) for \(0 < v < u^*\). Therefore, \(x^* < \frac{1}{2a(v)h}\) is a sufficient condition for (27) being hold. Here we complete the proof. \(\square\)

Proof of Proposition 4.1
Proof. The fact that \(u = 0\) is invariant and the population \(x\) is positive invariant in the state space, thus Model (3) is forward invariant in \(\mathbb{R}^2_+\) and \(\mathbb{R}_+ \times \mathbb{R}_-\). Since Model (3) has symmetric dynamics in \(\mathbb{R}^2_+\) versus in \(\mathbb{R}_+ \times \mathbb{R}_-\), we focus on the state space of \(\mathbb{R}^2_+\).

Let us define a new function \(\phi(x, u) = \frac{1}{xu}\) which is positive in \(\mathbb{R}^2_+\). Notice that \(u' = \frac{\partial H(x, u)}{\partial u}\) in Model (3), thus we have:

\[
\Delta(x, u) = \frac{\partial \phi(x, u) x H(x, u)}{\partial x} + \frac{\partial \phi(x, u) \frac{\partial H(x, u)}{\partial u}}{\partial u} = \frac{C_4 x^4 + C_3 x^3 + C_2 x^2 + C_1 x - \sigma_a^4 a(u) K(u) u^2}{x u K(u) (1 + ha(u)x)^3 \sigma_K^2 \sigma_a^2},
\]

where

\[
C_4 = -r h^3 \sigma_a^4 a(u)^3 (\sigma_K + u^2), \quad C_3 = -r h^2 \sigma_a^4 a(u)^2 (\sigma_K + u^2)
\]

\[
C_2 = h a u (\sigma_K^4 (h K(u) a^2 - 3r) - 3ru^2), \quad C_1 = \sigma_K^4 \sigma_a^4 (h K(u) a(u^2 - r) + \sigma_a^4 u^2 \left( h \left( \frac{\sigma_K}{\sigma_a} \right)^4 K(u) a(u^2 - r) \right)).
\]

This implies that \(\Delta(x, u) < 0\) if

\[
r > \max \left\{ h K_0 a_0^2 \left( \frac{\sigma_K}{\sigma_a} \right)^4 h K_0 a_0^2 \right\} \geq \max \left\{ h K_0 a^2(u), \left( \frac{\sigma_K}{\sigma_a} \right)^4 K(u) a(u^2) \right\} \text{ for } (x, u) \in \mathbb{R}^2_+.
\]

Similarly, we are able to show that \(\Delta(x, u) > 0\) for \((x, u) \in \mathbb{R}_+ \times \mathbb{R}_-\) if \(r > \max \left\{ h K_0 a_0^2, \left( \frac{\sigma_K}{\sigma_a} \right)^4 h K_0 a_0^2 \right\} \geq \max \left\{ h K_0 a^2(u), \left( \frac{\sigma_K}{\sigma_a} \right)^4 K(u) a(u^2) \right\}\). Therefore, by applying Dulac’s Criterion (Strogatz 1994), we can conclude that there is no limit cycle for Model (3) (i.e., only equilibrium dynamics) whenever the following equalities hold \(r > \max \left\{ h K_0 a_0^2, \left( \frac{\sigma_K}{\sigma_a} \right)^4 h K_0 a_0^2 \right\}\). \(\square\)
Proof of Proposition 4.2

Proof. The Darwinian dynamics (3) can be rewritten as follows by assuming general forms of $K(u), a(u)$:

$$
\frac{dx}{dt} = xG(v, u, x)|_{v=0} = x\left[r(1 - \frac{x}{K(u)}) - \frac{a(u)}{1 + ha(u)x}\right] = xH(u, x)
$$

$$
\frac{du}{dt} = \sigma^2 \frac{\partial G(v, u, x)}{\partial v}|_{v=0} = \sigma^2 \left[\frac{rK'(u)}{K^2(u)} - \frac{a'(u)}{1 + ha^2x}\right].
$$

(28)

Thus $(0, u^*)$ is an equilibrium of (28) if $a'(u^*) = 0$. The stability of $(0, u^*)$ is determined by the eigenvalues of the following Jacobian matrix evaluated at $(0, u^*)$

$$
J(x^*, u^*) = \left[\begin{array}{cc}
r - a(u^*) & 0 \\
\frac{rK'(u^*)}{K^2(u^*)} + 2\sigma^2 a(u^*) a'(u^*) & -\sigma^2 a''(u^*)
\end{array}\right].
$$

Thus, $(0, u^*)$ is locally asymptotically stable whenever the inequalities $r < a(u^*)$ and $a''(u^*) > 0$ holds. If the additional inequalities $r < a(u^*) \leq \max_{v \in \mathbb{R}}\{a(v)\}$ hold, then we have

$$
\max_{v \in \mathbb{R}}\{G(v, u^*, 0)\} = \max_{v \in \mathbb{R}}\{r - a(v)\} < 0.
$$

Thus, according to the definition of $(0, u^*)$ being ESS defined in Section 2, we can conclude that $(0, u^*)$ is an ESS of (28) if $a'(u^*) = 0$, $a''(u^*) > 0$ and $r < a(u^*) \leq \max_{v \in \mathbb{R}}\{a(v)\}$.

\[\Box\]

Acknowledgement

The authors would like to thank the comments of Professor Jim Cushing for the early draft of this manuscript. The research of Y.K. is partially supported by Simons Collaboration Grants for Mathematicians (208902), NSF DMS (1313312) and School of Letters and Sciences at ASU.

References


