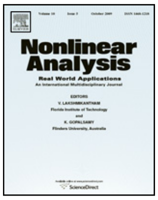
ARTICLE IN PRESS

Nonlinear Analysis: Real World Applications ▮ (▮▮▮▮) ▮▮▮–▮▮▮

Contents lists available at ScienceDirect

Nonlinear Analysis: Real World Applications

journal homepage: www.elsevier.com/locate/nonrwa



Weak Allee effects and species coexistence

Yun Kang [a,*], Abdul-Aziz Yakubu [b]

[a] *Applied Sciences and Mathematics, Arizona State University, Mesa, AZ 85212, USA*
[b] *Department of Mathematics, Howard University, Washington DC, 20059, USA*

ARTICLE INFO

Article history:
Received 9 April 2011
Accepted 31 May 2011

Keywords:
Ricker's model
Allee effects
Competition
Coexistence
Extinction
Permanence

ABSTRACT

In this article, we study the population dynamics of a two-species discrete-time competition model where each species suffers from either predator saturation induced Allee effects and/or mate limitation induced Allee effects. We focus on the following two possible outcomes of the competition: 1. one species goes to extinction; 2. the system is permanent. Our results indicate that, even if one species' intra-specific competition is less than its inter-specific competition, weak Allee effects induced by predation saturation can promote coexistence of the two competing species. This is supported by the outcome of two-species competition models without Allee effects. Also, we discuss our results and future work on multiple attractors in competition models with Allee effects.

Published by Elsevier Ltd

1. Introduction

The Allee effect and species competition are two basic ecological mechanisms that set lower and upper bounds on population density of species [1,2]. The Allee effect, defined as a reduced per-capita population growth rate at low densities, has important consequences for population dynamics and persistence. The effect can be caused by difficulties in finding a mate and predator avoidance or defense [3–6]. Competition for resources (e.g., food, space) may lead to lower population growth rate at high local population densities. Thus, small population density can be a result of competition among different species. Understanding the role of competition in populations subject to Allee effects can advance our understanding of extinction and establishment, with implications for conservation programs. However, the potential for synergism between the mechanisms generating the Allee effect and competition is not well understood and largely unconsidered [6,7].

In this article we investigate species extinction and permanence in discrete-time two-species competition models, where each species is subject to predator saturated and/or mate limitation induced Allee effects. One of our main findings is that predator saturated weak Allee effect can promote coexistence of two competing species; which is supported by two-species competition models without Allee effects. This result may have important implications for conservation programs, and can be considered as a complement to the current studies on population dynamics in the presence of Allee effects (e.g., [3,5,7–29]) as well as various models in patchy environment (e.g., [30–35]).

To study the extinction and permanence of discrete-time two-species competition models, we first start with a single-species discrete-time model that has a mechanism for generating Allee effects. There has been a great deal of literature on deriving population models with Allee effects (e.g., [36], [5, Chapter 7], [25,37]). Our two-species competition models are based on single-species population models that were introduced by Schreiber [5].

---

[*] Corresponding author.
E-mail addresses: yun.kang@asu.edu (Y. Kang), ayakubu@howard.edu (A.-A. Yakubu).

1468-1218/$ – see front matter. Published by Elsevier Ltd
doi:10.1016/j.nonrwa.2011.05.031

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

1.1. Single-species models with Allee effects

Consider a single-species population model of the form

$$N_{t+1} = N_t e^{r(1-N_t/K)} I(N_t) \tag{1}$$

where $I(N_t)$ represents a positive density-dependent factor and $e^{r(1-N_t/K)}$ represents a negative density-dependent factor; r and K represent the intrinsic growth rate and the carrying capacity of the population in the absence of the positive density dependence.

For convenience, let $h(N) = Ne^{r(1-N/K)}I(N) = Nu(N)$. Assume that there is a unique positive value C that leads to the maximum value $M = \max_{N\geq 0}\{h(N)\} = h(C)$. We say that a species suffers from *weak Allee effects* if $u(0) > 1$ and suffers from *strong Allee effects* if $u(0) < 1$ and there is a positive value A such that $u(N) < 1$ for $0 \leq N \leq A$ and $u(N) > 1$ for some $N > A$. The study by Schreiber [5] classified the dynamics of the single-species model (1) into the following scenarios:

Persistence: If $e^r I(0) > 1$ and $I(0) > 0$ for all $N > 0$; then for all positive initial densities the population persists.
Extinction: If $e^{r(1-N/K)}I(N) < 1$ for all $N \geq 0$, then extinction occurs for all initial population densities.

If, in addition, the population dynamics of (1) exhibits *strong Allee effects*, then under the assumption that the function $h(N)$ has a negative Schwartzian derivative (i.e. $\frac{h'''(x)}{h'(x)} - \frac{3h''(x)}{2h'(x)} < 0$) on the interval $[A, \infty)$, the study by [5] classifies the dynamics of (1) into the following two categories:

Bistability: If $M\,u(M) > A$, then there is an interval of initial population densities for which the population of (1) persists. For initial densities outside this interval, the population of (1) goes to extinction.
Essential extinction: If $M\,u(M) < A$, then for a randomly chosen initial condition, the population of (1) goes to extinction with probability one.

Next, we consider single-species population models with Allee effects that are caused by predation with saturating functional responses or mate limitation. The dynamics of these models fall into the categories of persistence, extinction, bistability and essential extinction depending on model parameters.

1.1.1. Predator induced Allee effect

Perhaps the most common Allee effect occurs in species subject to predation by a generalist predator with a saturating functional response [5]. To study Allee effects due to predator saturation, let $I(N) = e^{-\frac{m}{1+sN}}$ be the probability of escaping predation by a predator with a saturating functional response where m represents predation intensity and s is proportional to the handling time [38]. Non-dimensionalizing (1) by setting $x_t = N_t/K$ and $b = sK$ gives

$$x_{t+1} = x_t e^{r(1-x_t)-\frac{m}{1+bx_t}} \tag{2}$$

whose dynamics depends exclusively on the quantities r; b; and m. The basic dynamics of (2) can be summarized as follows from the results of Schreiber [5]:

Lemma 1.1 (*Equilibria of* (2))**.** *If $r > m$, the population of* (2) *persists for all initial densities. If $r < m$, then the zero equilibrium is always stable. In addition, if $r < m < \frac{r(b+1)^2}{4b}$ and $b > 1$, then* (2) *has two positive equilibria that can be expressed as follows:*

$$x = \frac{r(b-1) \pm \sqrt{r^2 - 4mbr + 2r^2b + r^2b^2}}{2rb}.$$

1.1.2. Mating induced Allee effect

For many sexually reproducing organisms, finding mates becomes more difficult at low densities. To model mate limitation, let $I(N) = \frac{sN}{sN+1}$ be the probability of finding a mate where s is an individual's searching efficiency [3,5,8,36]. Non-dimensionalizing (1) by setting $x_t = N_t/K$ and $b = sK$ gives

$$x_{t+1} = x_t e^{r(1-x_t)} \frac{bx_t}{1+bx_t} \tag{3}$$

whose dynamics are determined by the quantities r and sK. The basic dynamics of (3) can be summarized as follows:

Lemma 1.2 (*Equilibria of* (3))**.** *The zero equilibrium of* (3) *is always stable. If $\frac{be^{r-1}}{r} < 1$, then the population of* (2) *goes to extinction for all initial densities. If $\frac{e^{r-1}}{r} > \frac{1}{r} + \frac{1}{b}$, then* (3) *has two positive equilibria x^* that satisfy the following equation:*

$$x^* e^{r(1-x^*)} = x^* + \frac{1}{b}.$$

In this article, we are interested in studying how *Allee effects* affect the population dynamics of two competing species. More specifically, we explore the following ecological questions:

1. If the Allee effect occurs in each competitor, what are sufficient conditions that guarantee coexistence of the competing species?

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

2. If the Allee effect occurs in each competitor, what are sufficient conditions that lead to the extinction of at least one species?
3. Can the occurrence of Allee effects promote coexistence where there is extinction of a species in the absence of Allee effects?

The remaining of this article is organized as follows: In Section 2, we introduce our two-species competition models with Allee effects. In Section 3, we study a two-species competition model with Ricker's recruitments and without the occurrence of Allee effects in each competitor. In Section 4, we derive sufficient conditions that guarantees one species goes to extinction in the competition models introduced in Section 2 (Theorem 4.1). In Section 5, we obtain permanence of competition models subject to weak Allee effects (Corollary 5.1). In comparison with the results of competition models without Allee effects, we conclude that weak Allee effects can promote coexistence. Also, we discuss our results and the potential future work on multiple attractors of competition models with Allee effects.

2. A two-species competition model with Allee effects

Let $a_i, i = 1, 2$ be the inter-specific competition coefficients defining the equivalences between the two species. In the following three subsections, we introduce two competing species subject to Allee effects, where Allee effects are induced by predator saturation, mate limitations or the combination of these two factors.

2.1. Competition model with predator induced Allee effects

Model I: Competition between two species that are both subject to predations by different generalist predators with saturating functional responses can be modeled as:

$$x_{t+1} = x_t e^{r_1(1-x_t)-\frac{m_1}{1+b_1x_t}-a_1y_t} \tag{4}$$

$$y_{t+1} = y_t e^{r_2(1-y_t)-\frac{m_2}{1+b_2y_t}-a_2x_t} \tag{5}$$

where $r_i, i = 1, 2$ represent the intrinsic growth rates as well as intra-specific competition coefficients; $m_i, i = 1, 2$ represent predation intensities and $b_i, i = 1, 2$ represent the product of the proportional to the handling time and the carrying capacities.

The sufficient condition on the existence of interior equilibria of **Model I** when $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ can be stated as follows:

Proposition 2.1 (*Existence of Interior Equilibria*). *Assume that* $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$. *Then if* $r < m < \frac{(br+r+a)^2}{4b(r+a)}$ *and* $b > 1 + \frac{a}{r}$, ***Model I*** *has two positive symmetric interior equilibria* (p_1^*, p_1^*) *and* (p_2^*, p_2^*) *that can be expressed as follows:*

$$p_1^* = \frac{r(b-1)-a-\sqrt{(br+a+r)^2-4bm(r+a)}}{2b(r+a)} \quad \text{and} \quad p_2^* = \frac{r(b-1)-a+\sqrt{(br+a+r)^2-4bm(r+a)}}{2b(r+a)}.$$

If $m < \min\{\frac{(br+r+a)^2}{4b(r+a)}, r\}$, ***Model I*** *has only one symmetric interior equilibrium* (p_2^*, p_2^*).

Proof. If the interior equilibrium has the symmetric form (p^*, p^*), then it should satisfies the following equations:

$$r(1-p^*) - \frac{m}{1+bp^*} - ap^* = 1 \Rightarrow p^* = \frac{r(b-1)-a \pm \sqrt{(br+a+r)^2-4bm(r+a)}}{2b(r+a)}.$$

If $m < \frac{(br+r+a)^2}{4b(r+a)}$ and $m < r$, then

$$(br+a+r)^2 - 4bm(r+a) - (r(b-1)-a)^2 = 4b(r-m)(r+a) > 0.$$

Thus,

$$\frac{r(b-1)-a-\sqrt{(br+a+r)^2-4bm(r+a)}}{2b(r+a)} < 0.$$

This implies that **Model I** has only one symmetric interior equilibrium (p_2^*, p_2^*) where

$$p_2^* = \frac{r(b-1)-a+\sqrt{(br+a+r)^2-4bm(r+a)}}{2b(r+a)} > 0.$$

Therefore, the statement regarding **Model I** holds. □

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Note: **Model I** has no non-symmetric interior equilibrium point if $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ and $r < a$. If this is not true, then let $(x^*, y^*), x^* \neq y^*$ be the interior equilibrium of **Model I** which satisfies the following equations:

$$r(1-x^*) - \frac{m}{1+bx^*} = ay^* \quad \text{and} \quad r(1-y^*) - \frac{m}{1+by^*} = ax^*. \tag{6}$$

Define a map $H : \mathbb{R}_+ \to \mathbb{R}_+$, where $H(x) = \frac{r(1-x)}{a} - \frac{m}{a(1+bx)}$. Eqs. (6) hold only if there is some x in the interval of

$$\frac{r(b-1) - \sqrt{(br+r)^2 - 4bmr}}{2br} < x < \frac{r(b-1) + \sqrt{(br+r)^2 - 4bmr}}{2br}$$

such that $\frac{dH}{dx} \leq -1$. However,

$$\frac{dH}{dx} = -\frac{r}{a} + \frac{bm}{a(1+bx)^2} > -\frac{r}{a} > -1.$$

Thus, **Model I** has no non-symmetric interior equilibrium point if $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ and $r < a$. In addition, Proposition 2.1 suggests that two competing species subject to strong Allee effects need larger b in order to coexist since the sufficient condition for one-species model to have possible locally stable interior equilibrium point is (from Lemma 1.1)

$$r < m < \frac{r(b+1)^2}{4b} \quad \text{and} \quad b > 1.$$

2.2. Competition model with mating induced Allee effects

Model II: Competition between two species that both are subject to mate limitation can be modeled as

$$x_{t+1} = x_t e^{r_1(1-x_t)-a_1 y_t} \frac{b_1 x_t}{1+b_1 x_t} \tag{7}$$

$$y_{t+1} = y_t e^{r_2(1-y_t)-a_2 x_t} \frac{b_2 y_t}{1+b_2 y_t} \tag{8}$$

where $r_i, i = 1, 2$ represent the intrinsic growth rates as well as intra-specific competition coefficients and $b_i, i = 1, 2$ represent the product of an individual's searching efficiency and the carrying capacities.

The sufficient condition on the existence of interior equilibria of **Model II** when $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$ can be stated as follows:

Proposition 2.2 (*Existence of Interior Equilibria*)**.** *Assume that* $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$. *Then if* $\frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}$, *then* ***Model II*** *has two symmetric interior equilibria* (p^*, p^*) *such that the following equation holds*

$$p^* e^{r(1-p^*)-ap^*} = p^* + \frac{1}{b}.$$

Proof. Since $r_i = r < m_i = m, a_i = a, b_i = b, i = 1, 2$, then the interior equilibrium has the symmetric form (p^*, p^*) which satisfies the following equations:

$$p^* e^{r(1-p^*)-ap^*} = p^* + \frac{1}{b}.$$

Let p_c to be the critical point of $pe^{r(1-p)-ap}$, i.e. $p_c = \frac{1}{r+a}$. Then from Fig. 1, we can conclude that **Model II** has two interior equilibria if

$$p_c e^{r(1-p_c)-ap_c} = \frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}.$$

Therefore, the statement regarding **Model II** holds. □

Note: Proposition 2.2 suggests that two competing species subject to strong Allee effects may also need larger b in order to coexist since the sufficient condition for one-species model to have possible locally stable interior equilibrium point is (from Lemma 1.2)

$$\frac{e^{r-1}}{r} > \frac{1}{r} + \frac{1}{b}.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

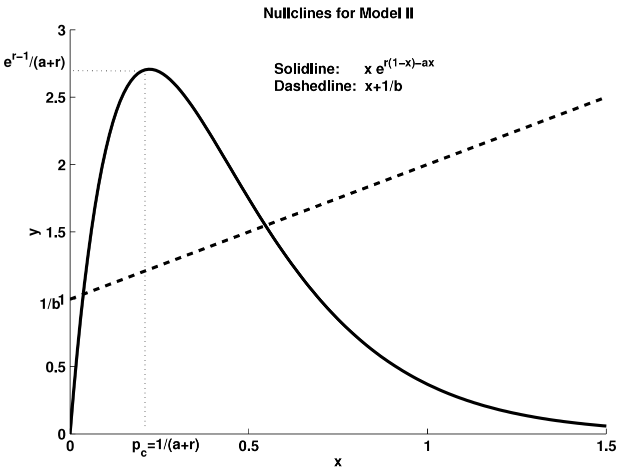
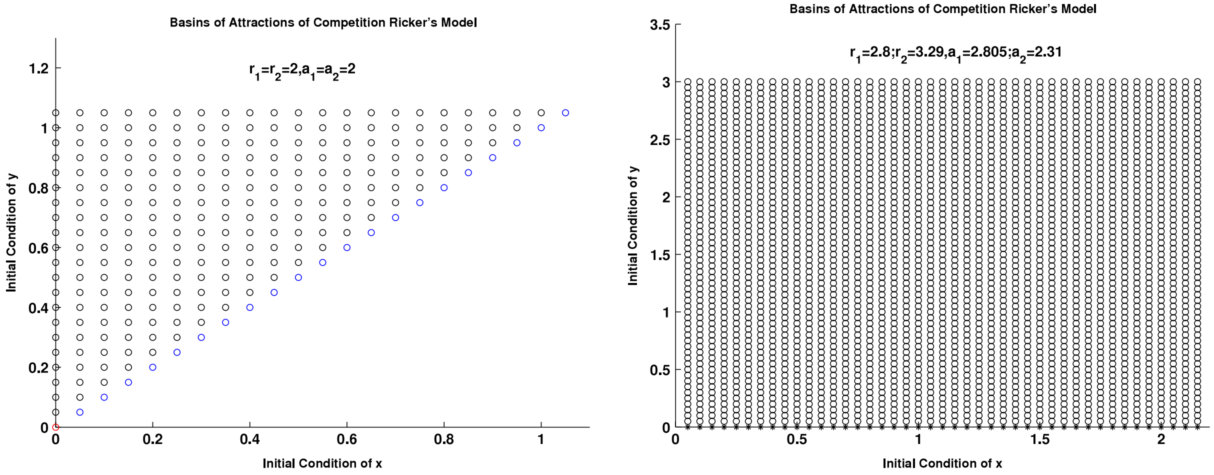


Fig. 1. Nullclines of **Model II** when $r_i = r < m_i = m$, $a_i = a$, $b_i = b$, $i = 1, 2$ and $\frac{e^{r-1}}{r+a} > \frac{1}{r+a} + \frac{1}{b}$.



(a) Basins of attraction of boundary attractors when $r_1 = r_2 = 1.5$, $a_1 = a_2 = 2$ for the system (17)–(18).

(b) Basins of attraction of boundary attractors when $r_1 = 2.8$, $r_2 = 3.29$, $a_1 = 2.805$, $a_2 = 2.31$ for the system (17)–(18).

Fig. 2. The basins of attraction of attractors on x-axis are the white region and the basins of attraction of attractors on y-axis are the region with black open circles. The coexistence region is the area with blue open circles. The extinction region is the area with red open circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. *Competition model with mixed Allee effects*

Model III: Competition between a species x subject to predation by a generalist predator with a saturating functional response and a species y subject to mate limitation can be modeled as:

$$x_{t+1} = x_t e^{r_1(1-x_t) - \frac{m}{1+b_1 x_t} - a_1 y_t} \tag{9}$$

$$y_{t+1} = y_t e^{r_2(1-y_t) - a_2 x_t} \frac{b_2 y_t}{1 + b_2 y_t} \tag{10}$$

where $r_i, i = 1, 2$ represent the intrinsic growth rates as well as intra-specific competition coefficients; m represents predation intensity for species x; b_1 represents the product of the proportional to the handling time and the carrying capacity of species x; b_2 represents the product of an individual's (species y) searching efficiency and the carrying capacity of species y.

If (x^*, y^*) is an interior equilibrium of **Model III**, then it should satisfy the following equations:

$$e^{r_1(1-x^*) - \frac{m}{1+b_1 x^*} - a_1 y^*} = 1 \quad \text{and} \quad e^{r_2(1-y^*) - a_2 x^*} \frac{b_2 y^*}{1 + b_2 y^*} = 1. \tag{11}$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

If b_2 is too small, e.g., $\frac{b_2 e^{r_2-1}}{r_2} < 1$, then **Model III** has no interior point since

$$y_{t+1} = y_t e^{r_2(1-y_t)-a_2 x_t} \frac{b_2 y_t}{1+b_2 y_t} \le y_t \max_{y>0}\{b_2 y e^{r_2(1-y)}\} \le y_t \frac{b_2 e^{r_2-1}}{r_2} < y_t.$$

2.4. A general two-species competition model subject to Allee effects

Based on the derivations of two-species competition models with Allee effects induced by the different mechanisms in the previous subsections, we now derive a general two-species competition model with Allee effects.

Let x_t and y_t be the population density of two competing in season t, then their population dynamics without Allee effects can be described by

$$x_{t+1} = x_t f(x_t, y_t) \tag{12}$$
$$y_{t+1} = y_t g(x_t, y_t) \tag{13}$$

where f and g are per-capita growth rates of species x, y respectively that satisfy the following two conditions:

Condition **H1**: Both $f(x, y)$ and $g(x, y)$ are strictly positive and twice differentiable in $\mathbb{R}^2_+$ with

$$f(0, 0) > 1 \quad \text{and} \quad g(0, 0) > 1.$$

Condition **H2**:

$$\lim_{x\to\infty} f(x, 0) = a_1 < 1, \quad \frac{\partial f(x, y)}{\partial x} < 0, \quad \frac{\partial f(x, y)}{\partial y} < 0$$
$$\lim_{x\to\infty} g(0, y) = a_1 < 1, \quad \frac{\partial g(x, y)}{\partial x} < 0, \quad \frac{\partial g(x, y)}{\partial y} < 0.$$

Then according to Lemmas 3.1 and 3.2 [39], we have the following properties of the competition model (12)–(13):

1. System (12)–(13) is dissipative, i.e., (12)–(13) has a compact attractor in $\mathbb{R}^2_+$ that attracts all points in $\mathbb{R}^2_+$:
$$\limsup_{t\to\infty} \max\{x_t, y_t\} < B$$
for any initial condition $(x_0, y_0) \in \mathbb{R}^2_+$ and B is some positive number.
2. Both species x and y are persistent and have only one nontrivial equilibrium point $(x^*, 0)$, $(0, y^*)$ in their single-species state (i.e., other species is absent), i.e., for any initial condition $(x_0, 0)$ and $(0, y_0)$ with $x_0 > 0, y_0 > 0$, there exists positive numbers $0 < b < B$ such that
$$b \le \liminf_{t\to\infty} \min\{x_t, y_t\} \le \limsup_{t\to\infty} \max\{x_t, y_t\} \le B.$$

If both species x and y suffer from Allee effects, then their population dynamics can be represented by

$$x_{t+1} = x_t f(x_t, y_t) I^x(x_t) \tag{14}$$
$$y_{t+1} = y_t g(x_t, y_t) I^y(y_t) \tag{15}$$

where I^i, $i = x, y$ represents a positive density-dependent factor of species i which satisfies Condition **H3**:

Condition **H3**: I^i, $i = x, y$ is differentiable in $\mathbb{R}_+$ and

$$0 \le I^i(0) \le 1 \quad \text{with} \ \frac{dI^i(u)}{du} > 0, \ u \in \mathbb{R}_+, \ i = x, y.$$

For convenience, we define

$$X = \{(x, y) : x \ge 0, y \ge 0\}, \qquad S_x = \{(x, 0) : x \ge 0\}, \qquad S_y = \{(0, y) : y \ge 0\}$$

and

$$S = S_x \bigcup S_y, \qquad M = X \setminus S = \{(x, y) : x > 0, y > 0\}.$$

One of our main goals of this subsection is to derive a sufficient criterion that can lead to the permanence of (14)–(15) in X, i.e., (14)–(15) has a compact attractor in M that attracts all points in M:

$$b \le \liminf_{n\to\infty} \min\{x_n, y_n\} \le \limsup_{n\to\infty} \max\{x_n, y_n\} \le B$$

for any initial condition $(x_0, y_0) \in M$ and b, B are some positive numbers. First, we have the following dissipative results on (14)–(15):

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Lemma 2.1 (*Dissipative*)**.** *If the system (14)–(15) satisfies Condition* **H1**, **H2**, **H3**, *then it is positively invariant and dissipative in* X.

Proof. The positively invariant property of (14)–(15) is straight forward from the non-negativity and continuity properties of f, g, I^x, I^y. Since the system (14)–(15) satisfies Condition **H1**–**H2**, then according to Lemmas 3.1 and 3.2 [39], we have the system (12)–(13) is dissipative in X. Since the system (14)–(15) also satisfies Condition **H3**, then

$$\begin{aligned} x_{t+1} &= x_t f(x_t, y_t) I^x(x_t) \le x_t f(x_t, y_t) \\ y_{t+1} &= y_t g(x_t, y_t) I^y(y_t) \le y_t g(x_t, y_t). \end{aligned} \tag{16}$$

Therefore, the competitive system with Allee effects (14)–(15) is also dissipative in X according to (16). □

Theorem 2.1 (*Persistence and Extinction of Species in (14)–(15)*)**.** *Assume that the system (14)–(15) satisfies Condition* **H1**–**H3**. *Then we have the following two cases:*

1. *If* $f(0, 0) \limsup_{x\to\infty} I^x(x) < 1$ *and* $g(0, 0) \limsup_{y\to\infty} I^y(y) < 1$, *then both species of (14)–(15) go to extinct, i.e., for any initial condition* $(x_0, y_0) \in X$, *we have*

   $$\limsup_{t\to\infty} \max\{x_t, y_t\} = 0.$$

2. *If* $f(0, 0)I^x(0) > 1$ *and* $g(0, 0)I^y(0) > 1$, *then both species have nontrivial boundary equilibria, i.e., there exists* $x^* > 0$ *and* $y^* > 0$ *such that*

   $$f(x^*, 0)I^x(x^*) = 1 \quad \textit{and} \quad g(0, y^*)I^y(y^*) = 1$$

   and the total population of two species is persistent in X, *i.e., there exists some positive number* ϵ *such that for any initial condition* $(x_0, y_0) \in X \setminus \{(0, 0)\}$, *we have*

   $$\liminf_{t\to\infty} x_t + y_t \ge \epsilon.$$

Proof. Let $I^x = \limsup_{x\to\infty} I^x(x)$. Since the system (14)–(15) satisfies Condition **H1**–**H3**, thus we have

$$x_{t+1} = x_t f(x_t, y_t) I^x(x_t) \le x_t f(0, 0) \limsup_{x\to\infty} I^x(x) = f(0, 0)I^x x_t \le [f(0, 0)I^x]^t\, x_0.$$

If $f(0, 0)I^x < 1$, then

$$x_{t+1} \le [f(0, 0)I^x]^t\, x_0 \Rightarrow 0 \quad \text{as } t \to \infty.$$

Thus, $\limsup_{t\to\infty} x_t = 0$. Similarly, we can show that if

$$g(0, 0) \limsup_{y\to\infty} I^y(y) < 1, \qquad \text{then } \limsup_{t\to\infty} y_t = 0.$$

Therefore, the first part of Theorem 2.1 holds.

Now assume that $f(0, 0)I^x(0) > 1$ and $g(0, 0)I^y(0) > 1$, then we can conclude that $(0, 0)$ is a source. Let $K^\epsilon(0, 0) = \{(x, y) \in X : x + y \le \epsilon\}$. If $\epsilon > 0$ is small enough, then any point in $K^\epsilon(0, 0)$ will emit from $K^\epsilon(0, 0)$ in some future time. According to Lemma 2.1, the system (14)–(15) is dissipative in X, thus any initial point $(x_0, y_0) \in X \setminus \{(0, 0)\}$ will enter the compact set $A^\epsilon = \{(x, y) \in X : \epsilon \le x + y \le B\}$ in some future time.

Now define $C^\epsilon = \{(x, y) \in X : b^\epsilon \le x + y \le B\}$ where $b^\epsilon = \epsilon \min\{f(B, B)I^x(0), g(B, B)I^y(0)\}$. Let (x_t, y_t) be a point in C^ϵ, then we have $x_t + y_t \ge \epsilon$ and

$$\begin{aligned} x_{t+1} + y_{t+1} &= x_t f(x_t, y_t)I^x(x_t) + y_t g(x_t, y_t)I^y(y_t) \ge x_t f(B, B)I^x(0) + (\epsilon - x_t)g(B, B)I^y(0) \\ &\ge \epsilon \min\{f(B, B)I^x(0), g(B, B)I^y(0)\} = b^\epsilon. \end{aligned}$$

This indicates that any point in $X \setminus \{(0, 0)\}$ will enter A^ϵ in some future time and then will be trapped in C^ϵ for all future time. Therefore, given some ϵ small enough, then for any initial condition $(x_0, y_0) \in X \setminus \{(0, 0)\}$ we have

$$\liminf_{t\to\infty} x_t + y_t \ge \epsilon.$$

In addition, Condition **H2** implies that there exist some positive number L such that

$$f(L, 0)I^x(L) < 1 \quad \text{and} \quad g(0, L)I^x(L) < 1.$$

Then according to the continuity of (14)–(15), we can conclude that the condition $f(0, 0)I^x(0) > 1$ and $g(0, 0)I^y(0) > 1$ indicates that there exists $x^* > 0$ and $y^* > 0$ such that

$$f(x^*, 0)I^x(x^*) = 1 \quad \text{and} \quad g(0, y^*)I^y(y^*) = 1.$$

Therefore, Theorem 2.1 holds. □

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Note: The first part of Theorem 2.1 indicates that both species go to *extinction* when the max per-capita growth rates (i.e., $f(0,0)\limsup_{x\to\infty} I^x(x)$ and $g(0,0)\limsup_{y\to\infty} I^y(y)$) are less than one. We want to point out that if a species goes to *essential extinction* without other species presence, then this species may or may not go to *essential extinction* in the competition system (14)–(15). A direct corollary from Theorem 2.1 can be stated as follows:

Corollary 2.1 (*Persistence of* (12)–(13)). *Assume that the system* (12)–(13) *satisfies Condition* **H1**– **H2**. *Then the total population of two species is persistent in* X*, i.e., there exists a positive number* ϵ *such that for any initial condition* $(x_0, y_0) \in X \setminus \{(0,0)\}$*, we have*

$$\liminf_{t\to\infty} x_t + y_t \geq \epsilon.$$

Proof. This is straightforward from Theorem 2.2, thus we omit it. □

Theorem 2.2 (*Permanence of Two Species in* (14)–(15)). *Assume that the system* (14)–(15) *satisfies Condition* **H1**–**H3**. *Then the system* (14)–(15) *is permanent in* M *if the following conditions hold*

C1: $f(0,0)I^x(0) > 1$ *and* $g(0,0)I^y(0) > 1$;
C2: *Let* $(x^*, 0)$ *and* $(0, y^*)$ *be any nontrivial boundary equilibria of* (14)–(15)*, then* $f(0,y^*)I^xI(y^*) > 1$ *and* $g(x^*,0)I^y(x^*) > 1$;
C3: *Let* $F(x,y) = \ln f(x,y) + \ln I^x(x)$ *and* $G(x,y) = \ln g(x,y) + \ln I^y(y)$ *and* $(x^*, 0)$, $(0, y^*)$ *be some nontrivial boundary equilibria, then*

$$G_{xx}(x,0) - \frac{G_x(x^*,0)F_{xx}(x,0)}{F_x(x^*,0)} \geq 0, \quad \textit{for all } x > 0$$

and

$$F_{yy}(0,y) - \frac{F_y(0,y^*)G_{yy}(0,y)}{G_y(0,y^*)} \geq 0, \quad \textit{for all } y > 0.$$

Note: Theorem 2.2 answers the first question listed in the introduction, which is a special case of Theorem 3.1 of Kang [40]. Condition **H1**, **H2**, **H3**, **C1** in Theorem 2.2 covers Condition **H, G1** in Theorem 3.1 of Kang [40]. Condition **C2** covers Condition **G2**; Condition **C3** covers Condition **G3, G4**. We apply Theorem 2.2 to specific models in Section 6.

3. Two-species competition models without Allee effects

A two-species competition model with Ricker's recruitments can be modeled by the following equations:

$$x_{t+1} = x_t e^{r_1(1-x_t)-a_1y_t} \tag{17}$$

$$y_{t+1} = y_t e^{r_2(1-y_t)-a_2x_t} \tag{18}$$

where $r_i, i = 1, 2$ and $a_i, = 1, 2$ represent the intrinsic growth rates (also intra-specific competition coefficients) and the inter-specific competition coefficients for each species. The dynamics of the similar competition models as (17)–(18) have be studied by many researchers, e.g., [41–44]. In this section, we will only focus on the dynamics of (17)–(18) where at least one species goes to extinction. First, we have the following results regarding the existence of the interior point of (17)–(18).

Proposition 3.1 (*Local Stability of Interior Point of* (17)–(18)). *If* $r_i > a_i, i = 1, 2$ *or* $r_i < a_i, i = 1, 2$*, then the system* (17)–(18) *has a unique interior equilibrium point* $(x^*, y^*) = \left(\frac{r_2(r_1-a_1)}{r_1r_2-a_1a_2}, \frac{r_1(r_2-a_2)}{r_1r_2-a_1a_2}\right)$ *where* (x^*, y^*) *is locally unstable if* $r_i < a_i, i = 1, 2$ *and is locally stable if*

$$r_i > a_i,\ i = 1, 2, \quad \textit{and} \quad 2 > 2 + \frac{r_1r_2(r_1-a_1)(r_2-a_2)}{r_1r_2-a_1a_2} - \frac{r_1r_2(r_1+r_2-a_1-a_2)}{r_1r_2-a_1a_2}$$
$$> \left|2 - \frac{r_1r_2(r_1+r_2-a_1-a_2)}{r_1r_2-a_1a_2}\right|.$$

Proof. From the expression of the system (17)–(18), we know that the interior equilibrium (x^*, y^*) should satisfy the following equations:

$$r_1(1-x^*) - a_1y^* = 0 \quad \text{and} \quad r_2(1-y^*) - a_2x^* = 0.$$

We can solve the equations above to get $(x^*, y^*) = \left(\frac{r_2(r_1-a_1)}{r_1r_2-a_1a_2}, \frac{r_1(r_2-a_2)}{r_1r_2-a_1a_2}\right)$. This indicates that (17)–(18) has a unique interior equilibrium (x^*, y^*) if

$$r_i > a_i \quad \text{or} \quad r_i < a_i, i = 1, 2.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

The Jacobian matrix of (17)–(18) that is associated with the interior equilibrium (x^*, y^*) can be found as

$$J|_{(x^*,y^*)} = \begin{pmatrix} -r_1x^* + 1 & -a_1x^* \\ -a_2y^* & -r_2y^* + 1 \end{pmatrix}. \tag{19}$$

Thus, the two eigenvalues of (19) are

$$\lambda_1 = 1 - \frac{r_1x^* + r_2y^*}{2} - \frac{\sqrt{(r_1x^* - r_2y^*)^2 + 4a_1a_2x^*y^*}}{2},$$
$$\lambda_2 = 1 - \frac{r_1x^* + r_2y^*}{2} + \frac{\sqrt{(r_1x^* - r_2y^*)^2 + 4a_1a_2x^*y^*}}{2}.$$

Therefore, if $r_i < a_i$, $i = 1, 2$, then

$$(r_1x^* - r_2y^*)^2 + 4a_1a_2x^*y^* - (r_1x^* + r_2y^*)^2 = 4x^*y^*(a_1a_2 - r_1r_2) > 0.$$

This implies that

$$\lambda_2 = 1 - \frac{r_1x^* + r_2y^*}{2} + \frac{\sqrt{(r_1x^* - r_2y^*)^2 + 4a_1a_2x^*y^*}}{2} > 1.$$

Therefore, (x^*, y^*) is locally unstable.

From the expression of the two eigenvalues λ_i, $i = 1, 2$, we have

$$\lambda_1 + \lambda_2 = 2 - (r_1x^* + r_2y^*) = 2 - \frac{r_1r_2(r_1 + r_2 - a_1 - a_2)}{r_1r_2 - a_1a_2},$$
$$\lambda_1\lambda_2 = (r_1r_2 - a_1a_2)x^*y^* - r_1x^* - r_2y^* + 1 = \frac{r_1r_2(r_1 - a_1)(r_2 - a_2)}{r_1r_2 - a_1a_2} - \frac{r_1r_2(r_1 + r_2 - a_1 - a_2)}{r_1r_2 - a_1a_2} + 1.$$

Thus if $r_i > a_i$, $i = 1, 2$ and the following inequalities hold

$$2 > 2 + \frac{r_1r_2(r_1 - a_1)(r_2 - a_2)}{r_1r_2 - a_1a_2} - \frac{r_1r_2(r_1 + r_2 - a_1 - a_2)}{r_1r_2 - a_1a_2} > \left|2 - \frac{r_1r_2(r_1 + r_2 - a_1 - a_2)}{r_1r_2 - a_1a_2}\right|,$$

then (x^*, y^*) is locally stable according to Jury Test (p. 57, [45]). Therefore, the statement of Proposition 3.1 holds. □

Note: Proposition 3.1 indicates that system (17)–(18) has no interior equilibrium if ($r_1 > a_1$ and $r_2 < a_2$) or ($r_1 < a_1$ and $r_2 > a_2$) according to the expression of interior equilibrium

$$(x^*, y^*) = \left(\frac{r_2(r_1 - a_1)}{r_1r_2 - a_1a_2}, \frac{r_1(r_2 - a_2)}{r_1r_2 - a_1a_2}\right).$$

This suggests that when one-species intra-specific competition is larger than its inter-specific competition and the other species' intra-specific competition is less than its inter-specific competition, then there is no interior equilibrium point. More general results regarding Ricker's competition models have been studied by Luis et al. [44].

Now we prove the following theorem regarding competitive exclusion and bistability of (17)–(18).

Theorem 3.1 (*Extinction of One Species of* (17)–(18)). *The dynamics of* (17)–(18) *can be summarized as follows:*

Bistability: If $r_i < a_i$, $i = 1, 2$, then both x-axis and y-axis are attractors (i.e., both species cannot invade each other at their low densities). In particular, if $r_1 = r_2 = r < a_1 = a_2 = a$, then there exists some $\epsilon > 0$ such that for any initial condition $x_0 < y_0$, we have

$$\limsup_{t\to\infty} x_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} y_t \geq \epsilon;$$

and for any initial condition $x_0 > y_0$, we have

$$\limsup_{t\to\infty} y_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} x_t \geq \epsilon.$$

Competition exclusion: If $a_2 \leq r_1 < r_2 \leq a_1$, then there exists some $\epsilon > 0$ such that for any initial condition $(x_0, y_0) \in M$, we have

$$\limsup_{t\to\infty} x_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} y_t \geq \epsilon.$$

If $a_1 \leq r_2 < r_1 \leq a_2$, then there exists some $\epsilon > 0$ such that for any initial condition $(x_0, y_0) \in M$, we have

$$\limsup_{t\to\infty} y_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} x_t \geq \epsilon.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Local extinction: If $r_1 < a_1$ *and* $r_2 > a_2$*, then there exists some* $\epsilon > 0$*, for any initial condition such that* $\frac{x_0^{1/r_1}}{y_0^{1/r_2}} < 1$*, the following holds*

$$\limsup_{t\to\infty} x_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} y_t \geq \epsilon.$$

Similarly, if $r_1 > a_1$ *and* $r_2 < a_2$*, then for any initial condition* $\frac{y_0^{1/r_2}}{x_0^{1/r_1}} < 1$*, the following holds*

$$\limsup_{t\to\infty} y_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} x_t \geq \epsilon.$$

Proof. First notice that the system (17)–(18) is positively invariant and dissipative in X, i.e.,

$$\limsup_{t\to\infty} \max\{x_t, y_t\} \leq \max\left\{\frac{e^{r_1-1}}{r_1}, \frac{e^{r_2-1}}{r_2}\right\} = B.$$

If $r_i < a_i$, $i = 1, 2$, then apply the relative nonlinearity concept in the paper by Kang and Chesson [39] to obtain that the external Lyapunov exponent of y-axis is $r_1 - a_1 y|_{y=1} = r_1 - a_1 < 0$ and the external Lyapunov exponent of x-axis is $r_2 - a_2 x|_{x=1} = r_2 - a_2 < 0$. We can apply Theorem 2.18 in the paper by Hutson and Schmitt [46] to conclude that both x-axis and y-axis are attractors in the sense that the stable manifold of x and y-axis are neighborhood of both axes in X.

Now if $r_1 = r_2 = r < a_1 = a_2 = a$ and $x_0 < y_0$, then

$$\frac{x_1}{y_1} = \frac{x_0 e^{r(1-x_0)-a y_0}}{y_0 e^{r(1-y_0)-a x_0}} = \frac{x_0}{y_0} e^{(a-r)(x_0-y_0)} < \frac{x_0}{y_0} < 1.$$

By induction, we have

$$\frac{x_t}{y_t} < \frac{x_{t-1}}{y_{t-1}} < \cdots < \frac{x_0}{y_0}.$$

Thus, $\{\frac{x_t}{y_t}\}_{t=0}^{\infty}$ is a strictly decreasing sequence that converges to some point $a \in \mathbb{R}_+$, i.e.,

$$\lim_{t\to\infty} \frac{x_t}{y_t} = \alpha.$$

We claim that $\alpha = 0$. Suppose that $\alpha > 0$, then

$$\frac{1}{1/\alpha + 1} = \lim_{t\to\infty} \frac{1}{\frac{y_t}{x_t} + 1} = \lim_{t\to\infty} \frac{x_t}{y_t + x_t} \leq \lim_{t\to\infty} \frac{x_t}{y_t} = \alpha.$$

From the dissipativeness of (17)–(18) and Corollary 2.1, we have

$$\liminf_{t\to\infty} \frac{x_t}{2B} \leq \lim_{t\to\infty} \frac{x_t}{y_t + x_t} = \frac{\alpha}{1+\alpha} \leq \limsup_{t\to\infty} \frac{x_t}{\epsilon}.$$

This implies that species x is weakly persistent in X, i.e.,

$$\limsup_{t\to\infty} x_t \geq \frac{\alpha\epsilon}{1+\alpha} > 0.$$

However, this contradicts to the fact that $(0, 1)$ has a stable manifold in M since $r < a$. Therefore $\alpha = 0$. This indicates that

$$\lim_{t\to\infty} \frac{x_t}{x_t + y_t} = 0.$$

According to Corollary 2.1, we have $\liminf_{t\to\infty} x_t + y_t \geq \epsilon$, thus,

$$\limsup_{t\to\infty} x_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} y_t \geq \epsilon.$$

Apply the above argument to the case when $r_1 = r_2 = r < a_1 = a_2 = a$ and $x_0 > y_0$, then we can also show that

$$\limsup_{t\to\infty} y_t = 0 \quad \text{and} \quad \liminf_{t\to\infty} x_t \geq \epsilon.$$

Therefore, the first part of Theorem 3.1 holds.

Now assume that $a_2 \leq r_1 < r_2 \leq a_1$, then for any $(x_0, y_0) \in M$, we have

$$\frac{x_t}{y_t} = \frac{x_{t-1} e^{r_1(1-x_{t-1})-a_1 y_{t-1}}}{y_{t-1} e^{r_2(1-y_{t-1})-a_2 x_{t-1}}} = \frac{x_{t-1}}{y_{t-1}} e^{r_1-r_2+(r_2-a_1)y_{t-1}+(a_2-r_1)x_{t-1}} < \frac{x_{t-1}}{y_{t-1}} e^{r_1-r_2} < \frac{x_0}{y_0} e^{t(r_1-r_2)}.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Thus, $\lim_{t\to\infty}\frac{x_t}{y_t}=0$. Since $\liminf_{t\to\infty} x_t+y_t\geq\epsilon$, therefore,

$$\limsup_{t\to\infty} x_t=0 \quad\text{and}\quad \liminf_{t\to\infty} y_t\geq\epsilon.$$

Similarly, we can show that if $a_1\leq r_2<r_1\leq a_2$, then for any $(x_0,y_0)\in M$, we have

$$\limsup_{t\to\infty} y_t=0 \quad\text{and}\quad \liminf_{t\to\infty} x_t\geq\epsilon.$$

Now consider the case when $r_1<a_1$, $r_2>a_2$ and $\frac{x_0^{1/r_1}}{y_0^{1/r_2}}<1$. Then the system (17)–(18) has no interior equilibrium point according to Proposition 3.1; and the following inequalities hold

$$\frac{x_1^{1/r_1}}{y_1^{1/r_2}}=\frac{x_0^{1/r_1}e^{(1-x_0)-a_1y_0/r_1}}{y_0^{1/r_2}e^{(1-y_0)-a_2x_0/r_2}}=\frac{x_0^{1/r_1}}{y_0^{1/r_2}}e^{(a_1/r_1-1)x_0+(1-a_2/r_2)y_0}<\frac{x_0^{1/r_1}}{y_0^{1/r_2}}<1.$$

Thus,

$$\lim_{t\to\infty}\frac{x_t^{1/r_1}}{y_t^{1/r_2}}=0.$$

According to Corollary 2.1, we have $\liminf_{t\to\infty} x_t+y_t\geq\epsilon$, therefore,

$$\limsup_{t\to\infty} x_t=0 \quad\text{and}\quad \liminf_{t\to\infty} y_t\geq\epsilon.$$

Apply the above argument to the case when $r_1>a_1$, $r_2<a_2$ and $\frac{x_0^{1/r_1}}{y_0^{1/r_2}}>1$, then we can also show that

$$\limsup_{t\to\infty} y_t=0 \quad\text{and}\quad \liminf_{t\to\infty} x_t\geq\epsilon.$$

Therefore, the third part of Theorem 3.1 holds. □

Note: The first part of Theorem 3.1 indicates that both species cannot invade each other at low abundance levels when both species' intra-specific competition coefficients are less than inter-specific competition coefficients. The numerical simulations support that the system (17)–(18) indeed has bistability. We prove the bistability for the symmetric case (see Fig. 2(a)). Many studies (e.g., [42–44,47,48]) have more general results on competitive exclusion. The second part of Theorem 3.1 is a special case of theirs. For the asymmetrical case, e.g., when $r_1=2.8$, $r_2=3.29$, $a_1=2.805$, $a_2=2.31$, the third part of Theorem 3.1 combined with the numerical simulation Fig. 2(b) suggest that there is no coexistence if $a_2<r_1<a_1<r_2$. In addition, from Proposition 3.4(i) of [41], the symmetric form of (17)–(18) has no nontrivial period two points if the intrinsic growth rates are less than 2, i.e., $r\leq 2$.

4. Extinction of one species in the competition models with Allee effects

It is known that in two-species discrete-time Kolmogorov-type competition models such as system (12)–(13), the species with the larger per-capita growth rate drives the other to extinction. However, when the recruitment functions of the two species is Ricker's function, then the species that is always increasing (dominant species) when the other is increasing dominates the system and drives the weaker species to extinction [47,48].

4.1. Competition models with Allee effects

First notice that all two-species competition models with Allee effects (i.e., **Model I**, **Model II** and **Model III**) satisfy Condition **H1**, **H2**, **H3**. We have the following theorems regarding these models:

Theorem 4.1 (*Extinction of One Species*)**.** *For* ***Model I****,*

Bistability: Assume that $r_i=r$, $a_i=a$, $b_i=b$, $m_i=m$, $i=1,2$ *and* $r<a$, *then*

$$\limsup_{t\to\infty} x_t=0 \quad \text{if } x_0<y_0; \quad \text{and} \quad \limsup_{t\to\infty} y_t=0 \quad \text{if } x_0>y_0.$$

Extinction: If $a_2 \leq r_1 < r_2 \leq a_1$, $m_2 \leq m_1$ *and* $b_1 m_2 \leq b_2 m_1$, *then we have*

$$\limsup_{t\to\infty} x_t = 0 \quad \textit{if } x_0 < y_0.$$

If $a_1 \leq r_2 < r_1 \leq a_2$, $m_1 \leq m_2$ *and* $b_2 m_1 \leq b_1 m_2$, *then we have*

$$\limsup_{t\to\infty} y_t = 0 \quad \textit{if } y_0 < x_0.$$

*For **Model II**,*

Bistability: Assume that $r_i = r, a_i = a, b_i = b, i = 1, 2$ *and* $r < a$, *then*

$$\limsup_{t\to\infty} x_t = 0 \quad \textit{if } x_0 < y_0; \qquad \textit{and} \qquad \limsup_{t\to\infty} y_t = 0 \quad \textit{if } x_0 > y_0.$$

Extinction: If $a_2 \leq r_1 < r_2 \leq a_1$ *and* $b_1 \leq b_2$, *then we have*

$$\limsup_{t\to\infty} x_t = 0 \quad \textit{if } x_0 < y_0.$$

If $a_1 \leq r_2 < r_1 \leq a_2$ *and* $b_2 \leq b_1$, *then we have*

$$\limsup_{t\to\infty} y_t = 0 \quad \textit{if } y_0 < x_0.$$

*For **Model III**, if* $a_1 \leq r_2 < r_1 \leq a_2$ *and* $r_2 + m \leq r_1$, *then for any initial condition* $(x_0, y_0) \in M$, *we have*

$$\limsup_{t\to\infty} y_t = 0.$$

Proof. For **Model I**, if $r_i = r, a_i = a, b_i = b, m_i = m, i = 1, 2$ and $x_0 < y_0$, then

$$\frac{x_1}{y_1} = \frac{x_0}{y_0} e^{(r-a)(y_0-x_0)+\frac{m}{1+by_0}-\frac{m}{1+bx_0}} = \frac{x_0}{y_0} e^{\left(r-a-\frac{bm}{(1+bx_0)(1+by_0)}\right)(y_0-x_0)} < \frac{x_0}{y_0} < 1.$$

By induction, we have

$$\frac{x_t}{y_t} < \frac{x_{t-1}}{y_{t-1}} < \cdots < \frac{x_0}{y_0}.$$

Thus, $\{\frac{x_t}{y_t}\}_{t=0}^{\infty}$ is a strictly decreasing sequence that converges to some point $a \in \mathbb{R}_+$, i.e.,

$$\lim_{t\to\infty} \frac{x_t}{y_t} = \alpha < 1.$$

This indicates that if $\alpha > 0$, then

$$\left(r - a - \frac{bm}{(1+bx_t)(1+by_t)}\right)(y_t - x_t) = y_t \left(r - a - \frac{bm}{(1+bx_t)(1+by_t)}\right)\left(1 - \frac{x_t}{y_t}\right) \to 0 \quad \text{as } t \to 0.$$

Therefore,

$$\lim_{t\to\infty} y_t = 0 \quad \text{and} \quad \lim_{t\to\infty} x_t = 0.$$

If $\alpha = 0$, then for any positive integer N, there exist some $T_N > 0$ such that

$$\frac{x_t}{y_t} < \frac{1}{N} \quad \text{for all } t > T_N.$$

Assume that $\lim_{t\to\infty} x_t$ is not true, then there exists some $\delta > 0$ and a sequence $\{x_{t_i}\}_{i=1}^{\infty}$ such that

$$x_{t_i} > \delta \quad \text{and} \quad t_i \to \infty \quad \text{as } i \to \infty.$$

Thus, if $t_i > T_N$, we have

$$\frac{\delta}{y_{t_i}} < \frac{x_{t_i}}{y_{t_i}} < \frac{1}{N} \Rightarrow y_{t_i} > N\delta.$$

This indicates that $\limsup_{t\to\infty} y_t = \infty$ which is a contradiction to the fact that **Model I** is dissipative in X according to Lemma 2.1. Thus, $\lim_{t\to\infty} x_t = 0$. Similarly, we can show that $\lim_{t\to\infty} y_t = 0$ if

$$r_i = r, \qquad a_i = a, \qquad b_i = b, \qquad m_i = m, \qquad i = 1, 2, \qquad r < a \quad \text{and} \quad y_0 < x_0.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

If $a_2 \le r_1 < r_2 \le a_1,\ m_2 \le m_1$ and $b_1 m_2 \le b_2 m_1$, then

$$\frac{x_1}{y_1} = \frac{x_0}{y_0} e^{r_1 - r_2 + y_0(r_2 - a_1) + x_0(a_2 - r_1) + \frac{m_2 - m_1 + b_1 m_2 x_0 - b_2 m_1 y_0}{(1+b_2 y_0)(1+b_1 x_0)}} < \frac{x_0}{y_0} e^{r_1 - r_2} < 1 \quad \text{if } x_0 < y_0.$$

Thus by induction, we have

$$\frac{x_t}{y_t} < \frac{x_{t-1}}{y_{t-1}} e^{r_1 - r_2} < \frac{x_0}{y_0} e^{t(r_1 - r_2)} \to 0 \quad \text{as } t \to \infty.$$

Therefore, we have $\lim_{t\to\infty} x_t = 0$. Similarly, we can show that $\lim_{t\to\infty} y_t = 0$ if

$$a_1 \le r_2 < r_1 \le a_2, \qquad m_1 \le m_2, \qquad b_2 m_1 \le b_1 m_2 \quad \text{and} \quad y_0 < x_0.$$

For **Model II**, if $r_i = r$, $a_i = a$, $b_i = b$, $i = 1, 2$ and $r < a$, then

$$\frac{x_1}{y_1} = \frac{\frac{x_0}{1+bx_0}}{\frac{y_0}{1+by_0}} \frac{x_0}{y_0} e^{(r-a)(y_0 - x_0)}.$$

Since $I(x) = \frac{x}{1+bx}$ is an increasing function with respect to x, thus

$$\frac{I(x_0)}{I(y_0)} < 1 \quad \text{if } x_0 < y_0.$$

Therefore, we have

$$\frac{x_1}{y_1} = \frac{\frac{x_0}{1+bx_0}}{\frac{y_0}{1+by_0}} \frac{x_0}{y_0} e^{(r-a)(y_0 - x_0)} < \frac{x_0}{y_0} e^{(r-a)(y_0 - x_0)} < 1 \quad \text{if } x_0 < y_0.$$

By applying the similar arguments in proving the statement of **Model I**, we have

$$\limsup_{t\to\infty} x_t = 0 \quad \text{if } x_0 < y_0; \quad \text{and} \quad \limsup_{t\to\infty} y_t = 0 \quad \text{if } x_0 > y_0.$$

Now in the case that $a_2 \le r_1 < r_2 \le a_1$ and $b_1 \le b_2$, we have

$$\frac{x_1}{y_1} = \frac{\frac{b_1 x_0}{1+b_1 x_0}}{\frac{b_2 y_0}{1+b_2 y_0}} \frac{x_0}{y_0} e^{r_1 - r_2 + (r_2 - a_1) y_0 + (a_2 - r_1) x_0}.$$

Since $I(b, x) = \frac{bx}{1+bx}$ is an increasing function in x, b respectively, thus

$$\frac{I(b_1, x_0)}{I(b_2, y_0)} < 1 \quad \text{if } x_0 < y_0 \quad \text{and} \quad b_1 \le b_2.$$

Therefore, we have

$$\frac{x_1}{y_1} = \frac{\frac{b_1 x_0}{1+b_1 x_0}}{\frac{b_2 y_0}{1+b_2 y_0}} \frac{x_0}{y_0} e^{r_1 - r_2 + (r_2 - a_1) y_0 + (a_2 - r_1) x_0} < \frac{x_0}{y_0} e^{r_1 - r_2 + (r_2 - a_1) y_0 + (a_2 - r_1) x_0} < 1 \quad \text{if } x_0 < y_0.$$

Then by applying the similar arguments in proving the statement of **Model I**, we have

$$\limsup_{t\to\infty} x_t = 0 \quad \text{if } x_0 < y_0,\ a_2 \le r_1 < r_2 \le a_1,\ b_1 \le b_2$$

and

$$\limsup_{t\to\infty} y_t = 0 \quad \text{if } x_0 > y_0,\ a_1 \le r_2 < r_1 \le a_2,\ b_2 \le b_1.$$

For **Model III**, if $a_1 \le r_2 < r_1 \le a_2$ and $r_2 + m \le r_1$, then for any initial condition $(x_0, y_0) \in M$, we have

$$\frac{y_1}{x_1} = \frac{b_2 y_0}{1 + b_2 y_0} \frac{y_0}{x_0} e^{r_2 - r_1 + \frac{m}{1+b_2 x_0} + (a_1 - r_2) y_0 + (r_1 - a_2) x_0} < \frac{y_0}{x_0} e^{r_2 - r_1 + m + (a_1 - r_2) y_0 + (r_1 - a_2) x_0} < \frac{y_0}{x_0} e^{r_2 - r_1 + m} < 1.$$

Thus, by applying the similar arguments in proving the statement of **Model I**, we have

$$\lim_{t\to\infty} y_t = 0.$$

Therefore, the statement of Theorem 4.1 holds. $\square$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

Note: Theorem 4.1 answers the second question listed in the introduction for certain competition models with Allee effects. In general, if both species' intra-specific competition coefficients are less than the inter-specific competition coefficients, then the extinction of one species is more likely to happen. For **Model II** and **Model III**, if $\frac{b_1 e^{r_1-1}}{r_1} < 1$, then species x goes to extinction. Similarly, for **Model II**, if $\frac{b_2 e^{r_2-1}}{r_2} < 1$, then species y goes to extinction. In addition, Theorem 4.1 indicates that: 1. For symmetric cases, both **Model I** and **Model II** have neither coexistence of two species nor the locally stable interior equilibrium if the intra-specific competition coefficients are less than the inter-specific competition coefficients, i.e. $r < a$; 2. For asymmetric cases, the sufficient conditions of no coexistence of two species for all models need additional conditions as well as the intra-specific competition coefficients are less than the inter-specific competition coefficients, i.e. $r_i < a_i, i = 1, 2$. The additional conditions suggestion that it may be possible that **Model I**, **Model II** and **Model III** can have coexistence of two species even if $r_i < a_i, i = 1, 2$.

5. Weak Allee effects and permanence of Model I

The first part of Theorem 3.1 gives sufficient conditions when species x and y cannot coexist in the symmetric form of (17)–(18). In this section, we explore the possibility of the permanence of (4)–(5) when the competition model without Allee effects (17)–(18) does not have coexistence. A direct application of Theorem 2.2 to the system (4)–(5) can be summarized as the following corollary which is also a Corollary 5.2 in [40]:

Corollary 5.1. *System (4)–(5) is permanent if the following conditions hold*

Condition 1: $r_i > m_i, i = 1, 2.$
Condition 2: $f(0, y^*)I^x(y^*) > 1$ *and* $g(x^*, 0)I^y(x^*) > 1.$
Condition 3: $r_2 > \frac{b_2 m_2}{(1+b_2 y^*)^2}$ *and* $r_1 > \frac{b_1 m_1}{(1+b_1 x^*)^2}$

where $x^* = \frac{r_1(b_1-1)+\sqrt{r_1^2(1+b_1)^2-4m_1 b_1 r_1}}{2r_1 b_1}$ *and* $y^* = \frac{r_2(b_2-1)+\sqrt{r_2^2(1+b_2)^2-4m_2 b_2 r_2}}{2r_2 b_2}$.

Corollary 5.1 suggests that the competition without Allee effects (17)–(18) excludes coexistence but two competing species with weak Allee effects (4)–(5) may coexist. To illustrate this result, let us take a concrete example when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$.

First notice that the system (4)–(5) satisfies Condition **H1**, **H2**, **H3**. If $r_i > m_i, i = 1, 2$, then the boundary fixed points are

$$(0, 0), (x^*, 0) \quad \text{and} \quad (0, y^*)$$

where $x^* = \frac{r_1(b_1-1)+\sqrt{r_1^2(1+b_1)^2-4m_1 b_1 r_1}}{2r_1 b_1} = 0.942$ and $y^* = \frac{r_2(b_2-1)+\sqrt{r_2^2(1+b_2)^2-4m_2 b_2 r_2}}{2r_2 b_2} = 0.848$ when $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$.

Now define $F(x, y)$ and $G(x, y)$ as follows:

$$F(x, y) = r_1(1-x) - \frac{m_1}{1+b_1 x} - a_1 y \quad \text{and} \quad G(x, y) = r_2(1-y) - \frac{m_2}{1+b_2 y} - a_2 x.$$

Then $F(0, 0) = r_1 - m_1 = 2.4 > 0$ and $G(0, 0) = r_2 - m_2 = 2.34 > 0$, thus the system (4)–(5) satisfies Condition **C1**. In addition, we have the following:

$$F_x(x, 0) = -r_1 + \frac{b_1 m_1}{(1+b_1 x)^2}, \qquad F_{xx}(x, 0) = -\frac{2b_1^2 m_1}{(1+b_1 x)^3}, \qquad F_y(0, y) = -a_1, \qquad F_{yy}(0, y) = 0$$

$$G_x(x, 0) = -a_2, \qquad G_{xx}(x, 0) = 0, \qquad G_y(0, y) = -r_2 + \frac{b_2 m_2}{(1+b_2 y)^2}, \qquad G_{yy}(0, y) = -\frac{2b_2^2 m_2}{(1+b_2 y)^3}.$$

Notice that

$$F_{yy}(0, y) - \frac{F_y(0, y^*)G_{yy}(0, y)}{G_y(0, y^*)} = \frac{2a_1 b_2^2 m_2}{(r_2 - \frac{b_2 m_2}{(1+b_2 y^*)^2})(1+b_2 y)^3}$$

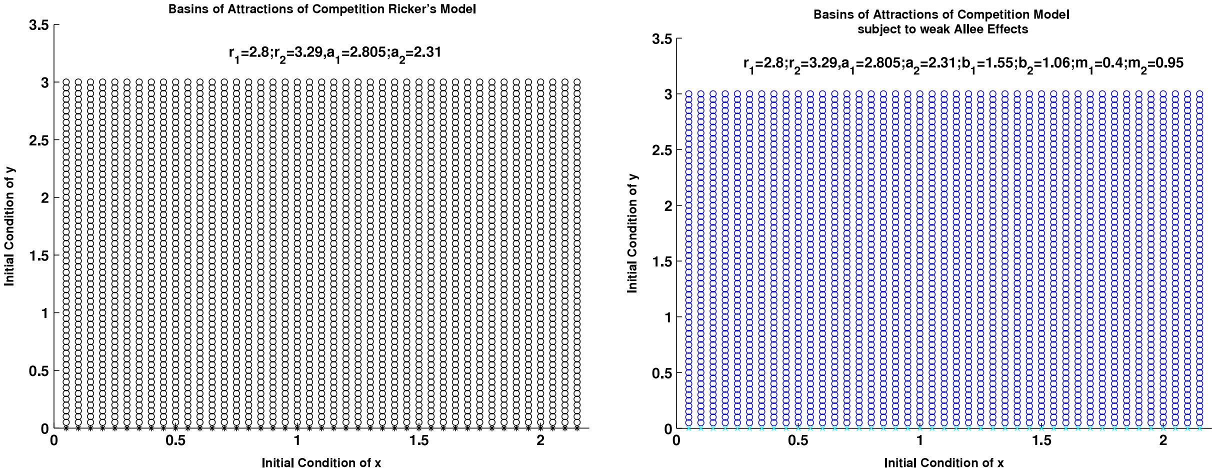
and

$$G_{xx}(x, 0) - \frac{G_x(x^*, 0)F_{xx}(x, 0)}{F_x(x^*, 0)} = \frac{2a_2 b_1^2 m_1}{(r_1 - \frac{b_1 m_2}{(1+b_1 x^*)^2})(1+b_1 x)^3},$$

thus, the signs of the above two equations are determined by the signs of $r_2 - \frac{b_2 m_2}{(1+b_2 y^*)^2}$ and $r_1 - \frac{b_1 m_2}{(1+b_1 x^*)^2}$. When $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$, we have

$$r_2 - \frac{b_2 m_2}{(1+b_2 y^*)^2} = 3.011 > 0 \quad \text{and} \quad r_1 - \frac{b_1 m_2}{(1+b_1 x^*)^2} = 2.698 > 0.$$

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031



(a) Basins of attraction of boundary attractors when $r_1 = 2.8$, $r_2 = 3.29$, $a_1 = 2.805$, $a_2 = 2.31$ for the system (17)–(18).

(b) Basins of attraction of boundary attractors when $r_1 = 2.8$, $r_2 = 3.29$, $a_1 = 2.805$, $a_2 = 2.31$, $b_1 = 1.55$, $b_2 = 1.06$, $m_1 = 0.4$, $m_2 = 0.95$ for the system (4)–(5).

Fig. 3. The basins of attraction of attractors on y-axis are the region with black open circles. The coexistence region is the area with blue open circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In addition, we have

$$F(0, y^*) = 0.164 > 0 \quad \text{and} \quad G(x^*, 0) = 0.022 > 0.$$

Therefore, the system (4)–(5) satisfies Condition **C2, C3**. Thus, according to Theorem 2.2, we can conclude that the system (4)–(5) is permanent in M in the case that $r_1 = 2.8, r_2 = 3.29, a_1 = 2.805, a_2 = 2.31, b_1 = 1.55, b_2 = 1.06, m_1 = 0.4, m_2 = 0.95$. Numerical simulation Fig. 3(b) supports our conclusion. However, according to the third part of Theorem 3.1 indicates that the competition without Allee effects (17)–(18) cannot coexist when the density of species x is low since $r_1 = 2.8 < a_1 = 2.805$ and its numerical simulation Fig. 3(a) suggests that species x goes to extinction for all initial conditions taken in M. Thus, we are able to conclude that weak Allee effects induced by predator saturation can promote the coexistence of two species, which answers the third question listed in the introduction.

The ecological implication of Corollary 5.1 and the concrete example above is that weak Allee effects decrease the fitness of species x (or species y) such that the other species y (or species x) is able to invade at the low density of species y (or species x).

In addition, we conclude that competition models with Allee effects induced by mate limitations cannot be permanent (e.g., **Model II** and **Model III**). This is due to the fact that the per capital growth rate of species that suffers from Allee effects induced by mate limitation is less than 1 at low densities, e.g.,

$$e^{r_2(1-y_t)-a_2x_t}\frac{b_2y_t}{1+b_2y_t} < b_2y_te^{r_2-a_2x_t} \to 0 \quad \text{as } y_t \to 0.$$

6. Discussion

In this paper, we study the extinction of one species and the permanence of two-species competition models that have Allee effects induced by predator saturation and/or mate limitations. Our analytical results indicate that a species tends to go extinct if its intra-specific competition is less than its inter-specific competition for both competition models with or without Allee effects. We are able to show competition exclusion for Ricker's competition model without Allee effects: species y out compete species x when species y's intra-specific competition coefficient r_2 is greater than species x's inter-specific competition coefficient a_2 but less than species x's intra-specific competition r_1 and its own inter-specific competition coefficient a_2, and in addition, species x's intra-specific competition coefficient r_1 is greater than its inter-specific competition coefficient a_1, i.e., $a_1 \le r_2 < r_1 \le a_2$. Moreover, our results show that if the intra-specific competition coefficient of one species is less than its inter-specific competition coefficient, e.g., $a_2 < r_1 < a_1 < r_2$, then a two-species competition model with weak Allee effects induced by predator saturation can still be permanent while its corresponding two-species competition model without Allee effects is not permanent according to Theorem 4.1 and even does not have coexistence (see Fig. 3(a)). This result implies that weak Allee effects can promote coexistence of two competing species. The biological explanation for this phenomenon is that weak Allee effects decrease the fitness of species x (or species y) such that the other species y (or species x) is able to invade at low densities of species y (or species x).

We summarize our findings as follows: In Theorem 2.2, we obtain sufficient conditions that guarantee coexistence of the two competing species each of which is subject to an Allee effect. In Theorems 2.1 and 4.1, we obtain sufficient conditions

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031

that lead to the extinction of at least one species when the Allee effect occurs in each competitor. In Section 5, we provide a concrete example based on 5.1 to illustrate the occurrence of the Allee effect can promote coexistence where there is extinction of a species in the absence of Allee effects.

The full dynamics of all three models introduced in this article (i.e., **Model I**, **Model II** and **Model III**) can be very complicated due to two factors; model structure and Allee effects. It is well known that population models with Allee effects can have multiple attractors for both continuous and discrete-time cases (e.g., [18,25,30–32,34,35,47–49]). It will be interesting to explore how different Allee effects combined with inter-specific competition affect the number of attractors and their basins of attractions. In addition, the study by Gyllenberg et al. [32] on metapopulation two-patch models subject to Allee effects and competition suggests that Allee effect and the non-local competition can conserve spatial heterogeneity (there exist stable equilibria with unequal population densities in the two patches) as well as create heterogeneity (instability of the equilibrium with equal population densities in two patches). The competition between two species in our models can be analogous to the dispersal between two patches. Thus, we can expect to have similar phenomena in terms of conserving heterogeneity (there exist stable equilibria with unequal population densities for two species) as well as creating heterogeneity (instability of the equilibrium with equal population densities in two species).

In addition, it will also be interesting to explore the following questions:

1. When does strong Allee effects promote species coexistence where there is a species extinction without it?
2. Can competition rescue an endangered species from *essential extinction* due to strong Allee effects?

Acknowledgments

The research of Y. Kang has been partially supported by SSE grant from CTI of Arizona State University. The research of A-A. Yakubu has been partially supported by the Mathematical Biosciences Institute of The Ohio State University, Department of Homeland Security, DIMACS and CCICADA of Rutgers University and the National Science Foundation through Award 0832782.

References

[1] M. Begon, J.L. Harper, C.R. Townsend, Ecology. Individuals, Populations and Communities, third edition, Blackwell Science, Oxford, 1996.
[2] R. Etiemme, B. Werthei, Hemerik L. Schneider, J. Powell, The interaction between dispersal, the Allee effect and scramble competition affects population dynamics, Ecological Modeling 148 (2002) 153–168.
[3] M.A. McCarthy, The Allee effect, finding mates and theoretical models, Ecological Modelling 103 (1997) 99–102.
[4] P.A. Stephens, W.J. Sutherland, R.P. Freckleton, What is the Allee effect? Oikos 87 (1999) 185–190.
[5] S. Schreiber, Allee effects, extinctions, and chaotic transients in simple population models, Theoretical Population Biology 64 (2003) 201–209.
[6] F. Courchamp, L. Berec, J. Gascoigne, Allee Effects in Ecology and Conservation, Oxford University Press, 2009.
[7] S.R. Zhou, C.Z. Liu, G. Wang, The competitive dynamics of metapopulation subject to the Allee-like effect, Theoretical Population Biology 65 (2004) 29–37.
[8] B. Dennis, Allee effects: population growth, critical density, and the chance of extinction, Natural Resource Modeling 3 (1989) 481–538.
[9] B. Dennis, Allee effects in stochastic populations, Oikos 96 (2002) 389–401.
[10] J.F. Selgrade, G. Namkoong, Dynamical behavior for population genetics models of differential and difference equations with nonmonotone fitnesses, Journal of Mathematical Biology 30 (1992) 815–826.
[11] N. Shigesada, K. Kawasaki, Introduction, in: N. Shigesada, K. Kawasaki (Eds.), Biological Invasions: Theory and Practice, Oxford University Press, New York, USA, 1997, pp. 1–5.
[12] C. Greene, J.A. Stamps, Habitat selection at low population densities, Ecology 82 (2001) 2091–2100.
[13] T.H. Keitt, M.A. Lewis, R.D. Holt, Allee effects, invasion pinning, and species' borders, The American Naturalist 157 (2001) 203–216.
[14] W.F. Fagan, M.A. Lewis, M.G. Neubert, Driessche P. van den, Invasion theory and biological control, Ecology Letters 5 (2002) 148–157.
[15] M.H Wang, M. Kot, M.G. Neubert, Integrodifference equations, Allee effects, and invasions, Journal of Mathematical Biology 44 (2002) 150–168.
[16] A. Liebhold, J. Bascompte, The Allee effect, stochastic dynamics and the eradication of alien species, Ecology Letters 6 (2003) 133–140.
[17] J.M. Drake, Allee effects and the risk of biological invasion, Risk Analysis 24 (2004) 795–802.
[18] S. Petrovskii, A Morozov, B.-L. Li, Regimes of biological invasion in a predator–prey system with the Allee effect, Bulletin of Mathematical Biology 67 (2005) 637–661.
[19] C.M. Taylor, A. Hastings, Allee effects in biological invasions, Ecology Letters 8 (2005) 895–908.
[20] S.R.J. Jang, Allee effects in a discrete-time host-parasitoid model, Journal of Difference Equations and Applications 12 (2006) 165–181.
[21] P. Aguirre, E. González-Olivares, E. Sáez, Two limit cycles in a Leslie-Gower predator–prey model with additive Allee effect, Nonlinear Analysis: Real World Applications 10 (2009) 1401–1416.
[22] C. Egami, Positive periodic solutions of nonautonomous delay competitive systems with weak Allee effect, Nonlinear Analysis: Real World Applications 10 (2009) 494–505.
[23] C. Egami, Permanence of delay competitive systems with weak Allee effects, Nonlinear Analysis: Real World Applications 11 (2010) 3936–3945.
[24] H. Thieme, T. Dhirasakdanon, Z. Han, R. Trevino, Species decline and extinction: synergy of infectious disease and Allee effect? Journal of Biological Dynamics 3 (2009) 305–323.
[25] S.N. Elaydi, R.J. Sacker, Population models with Allee effect: a new model, Journal of Biological Dynamics 4 (2010) 397–408.
[26] J.J. Nieto, M.V. Otero-Espinar, R. Rodríguez-López, Dynamics of the fuzzy logistic family, in: Discrete and Continuous Dynamical Systems: Series B, vol. 14, 2010, pp. 699–717.
[27] S. Padhi, P.D.N. Srinivasu, G. Kumar Kiran, Periodic solutions for an equation governing dynamics of a renewable resource subjected to Allee effects, Nonlinear Analysis: Real World Applications 11 (2010) 2610–2618.
[28] L.M. Wang, L-S. Chen, J.J Nieto, The dynamics of an epidemic model for pest control with impulsive effect, Nonlinear Analysis: Real World Applications 11 (2010) 1374–1386.
[29] J. Liu, D. Wang, Z Teng, The persistence and global attractivity in general nonautonomous discrete single-species Kolmogorov model with delays, Journal of Mathematical Analysis and Applications 378 (2011) 403–417.
[30] P. Amarasekare, Allee effects in metapopulation dynamics, The American Naturalist 152 (1998) 298–302.
[31] P. Amarasekare, Interactions between local dynamics and dispersal: insights from single species models, Theoretical Population Biology 53 (1998) 44–59.

[32] M. Gyllenberg, J. Hemminki, T. Tammaru, Allee effects can both conserve and create spatial heterogeneity in population densities, Theoretical Population Biology 56 (1999) 231–242.
[33] A.S. Ackleh, L.J.S Allen, J. Carter, Establishing a beachhead: a stochastic population model with an Allee effect applied to species invasion, Theoretical Population Biology 71 (2007) 290–300.
[34] Y. Kang, N. Lanchier, Expansion or extinction: deterministic and stochastic two-patch models with Allee effects, Journal of Mathematical Biology 62 (6) (2011) 925–973.
[35] Y. Kang, D. Armbruster, Dispersal effects on a two-patch discrete model for plant-herbivore interactions, Journal of Theoretical Biology 268 (2011) 84–97.
[36] I. Scheuring, Allee effect increases dynamical stability in populations, Journal of Theoretical Biology 199 (1999) 407–414.
[37] H. Thieme, Mathematics in Population Biology, Princeton University Press, Princeton, 2003.
[38] M.P. Hassell, J.H. Lawton, J.R. Beddington, The components of arthropod predation: I. The prey death-rate, Journal of Animal Ecology 45 (1976) 135–164.
[39] Y. Kang, P. Chesson, Relative nonlinearity and permanence, Theoretical Population Biology 78 (2010) 26–35.
[40] Y. Kang, 2011, Permanence of a general discrete two-species interaction model with non-monotonic per capita growth rates, 2011, Preprint.
[41] H. Jiang, T.D. Rogers, The discrete dynamics of symmetric competition in the plane, Journal of Mathematical Biology 25 (1987) 573–596.
[42] J. Cushing, S. Levarge, N. Chitnis, S.M. Henson, Some discrete competition models and competitive exclusion principle, Journal of Difference Equations and Applications 10 (2004) 1139–1151.
[43] J. Cushing, S.M. Henson, C.C. Blackburn, Multiple mixed-type attractors in a competition model, Journal of Biological Dynamics 1 (2007) 347–362.
[44] R. Luis, S. Elaydi, H. Oliveira, 2011, Stability of a Ricker-type competition model and the competition exclusion principle. Journal of Biological Dynamics, in press (doi:10.1080/17513758.2011.581764).
[45] L. Edelstein-Keshet, Mathematical Models in Biology, SIAM, Philadelphia, 2005.
[46] V Hutson, K. Schmitt, Permanence and the dynamics of biological systems, Mathematical Biosciences 111 (1992) 1–71.
[47] J. Franke, A.-A. Yakubu, Global attractors in competitive systems, Nonlinear Analysis, Theory, Methods & Application 16 (1991) 111–129.
[48] J. Franke, A.-A. Yakubu, Mutual exclusion versus coexistence for discrete competitive systems, Journal of Mathematical Biology 30 (1991) 161–168.
[49] R. Luis, S. Elaydi, H. Oliveira, Nonautonomous periodic systems with Allee effects, Journal of Difference Equations and Applications 1 (2009) 1–16.

Please cite this article in press as: Y. Kang, A.-A. Yakubu, Weak Allee effects and species coexistence, Nonlinear Analysis: Real World Applications (2011), doi:10.1016/j.nonrwa.2011.05.031