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RESEARCH ARTICLE

Competitive exclusion and coexistence in a Lotka–Volterra competition model with Allee effects and stocking

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We propose a Lotka–Volterra competition model of two populations where one population is subject to Allee effects and is also under stocking to investigate competition outcomes. The resulting model is analysed by studying its global asymptotic dynamics. In some cases, the endangered population can drive the other population to extinction, while in other cases, the endangered population cannot survive. Coexistence of both competing populations is possible in some parameter regimes. It is concluded that considerable care must be taken before implanting the population that is subject to Allee effects.

Keywords: Lotka–Volterra competition model; Allee effects; stability; stocking

1. Introduction

The Allee effect, referring to the reduced fitness or the decline in population growth at low population densities or sizes, was first observed by Allee in the 1930s (Allee, 1938). It has significant impact on population survival when the population is at low level. There has been a rebound of interest in Allee effects recently due to fragmentation of habitats, invasions of exotic species, biological control of pests, etc. all involving small populations (Courchamp, Berec, & Gascoigne, 2008).

White abalone (*Haliotis sorenseni*) is the first marine invertebrate protected under the Endangered Species Act (Hobday & Tegner, 2000). At low population density, the population is subject to Allee effects due to failure of external fertilization (Hobday & Tegner, 2000). Natural recovery without intervention is unlikely to occur for the population, while strong degree of spawning synchrony and high fecundity of white abalone make captive breeding and stocking feasible (Stierhoff, Neuman, & Butler, 2012). A Leslie matrix model of white abalone is proposed in Li and Jiao (2015) to study different stocking strategies. Since populations in a natural environment are unlikely to be isolated, we propose a two-species competing model to investigate the effects of stocking when one of the populations is subject to Allee effects.

Many single-species and predator–prey models incorporating Allee effects have appeared in the literature, including Allen, Fagan, Hognas, and Fagerholm (2005), Cushing (1988), Dennis (2002), Hilker (2010), Morozov, Petrovskii, and Li (2004), Thieme, Dhirasakdanon, Han, and Trevino (2009), Voorn, Hemerik, Boer, and Kooi (2007), Zhou and Wang (2004) and Zhou, Liu, and Wang (2005). In each of these deterministic models, a critical threshold is observed below which the population will inevitably become extinct. Competition models with Allee effects on the other hand have not received much attention.

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The earliest research dates back to Wang, Liang, and Wang (1999), where a continuous-time Lotka–Volterra competition system with Allee effects occurring in both populations is studied.

Discrete-time competition models are proposed and analysed by Kang (2013) and Livadiotis and Elaydi (2012), where each population in the absence of the other population follows the growth of the Ricker model and is also subject to Allee effects. Chow and Jang (2014) study a discrete-time competition system based on the Leslie–Gower equation, where both populations are also subject to Allee effects. These competition models are discrete-time systems of difference equations (Chow & Jang, 2014; Kang, 2013; Livadiotis & Elaydi, 2012), which are adequate to model populations with non-overlapping generations. For example, many insects die after reproduction and many fishes have distinctive life stages, and discrete-time population models are appropriate to study these types of populations.

There are many other populations that reproduce continuously and therefore difference equations are not adequate to model such populations. In this study, we use ordinary differential equations to model population interaction and consequently individuals within each population are assumed to be homogeneous. We propose a model of two competing populations based on the classical Lotka–Volterra competition system where one population is subject to Allee effects, while the other population exhibits no Allee effects. However, our modelling aspect of Allee effects is different from that of Wang et al. (1999). It is expected that the population with Allee effects will become extinct if its population size is small. Consequently, a constant rate of the external population is input into the resident population to rescue the population (Hobday & Tegner, 2000; Nock et al., 2011). There are discrete-time mathematical models proposed to investigate the effects of external stocking. See AlSharawi and Rhouma (2009), Elaydi and Yakubu (2002), Kulenović and Nurkanović (2012), Chow and Jang (2015) and references cited therein. Continuous-time models incorporating stocking have been studied by Brauer and Soudack (1982) for a class of predator–prey systems. The effect of stocking is discussed (Brauer & Soudack, 1982) by comparing isoclines with the model of no stocking. In this study, we shall investigate the impact of stocking upon population persistence, extinction and competitive exclusion.

In the following section, we present the model and study its global asymptotic dynamics. It is proven that in some cases, the population with Allee effects can drive the other population to extinction, while in other cases, the endangered population cannot survive with stocking. Coexistence of both competing populations is possible in certain parameter regimes. The final section summarizes results and conclusions. The proofs of our main results are presented in the Appendix 1.

2. The model and asymptotic dynamics

Let $x(t)$ and $y(t)$ denote two competing populations at time $t \geq 0$. The well-known Lotka–Volterra competition model assumes that each population grows logistically to its carrying capacity in the absence of the other population (Allen, 2006):

$$\begin{aligned} x' &= r_1 x\left(1 - \frac{x}{K_1}\right) - \frac{r_1 c_1 x y}{K_1}, \\ y' &= r_2 y\left(1 - \frac{y}{K_2}\right) - \frac{r_2 c_2 x y}{K_2}, \end{aligned} \tag{2.1}$$

where competition coefficient $c_1 > 0$ represents the effect of population y on x and $c_2 > 0$ is the effect of population x on y. Parameters $r_i, K_i, c_i, i = 1, 2$, are positive constants, where r_1 and r_2 are the intrinsic growth rates of populations x and y, respectively, and K_1 and K_2 are the corresponding carrying capacities. The asymptotic dynamics of (2.1) are well known. For most of the parameter values, all solutions (or except possibly on a set of initial conditions of Lebesgue measure zero) converge to one of the boundary steady states (Allen, 2006). Only in a very small parameter, regime solutions converge to the coexisting steady state. These scenarios correspond to the classical competitive exclusion principle in population biology and therefore the system has been frequently used to illustrate the principle (Begon, Harper, & Townsend, 1996).

If population x is subject to Allee effects, then we model the population by the following equation prior to competition:

$$x' = r_1 x\left(1 - \frac{x}{K_1}\right)(x - a_1), \quad x(0) \geq 0, \tag{2.2}$$

where a_1, $0 < a_1 < K_1$, is the Allee threshold of the x population. Such an equation has been adopted by Amarasekare (1998) and Keitt, Lewis, and Holt (2001) to model Allee effects. It is easy to see that solutions $x(t)$ of (2.2) satisfy $\lim_{t\to\infty} x(t) = 0$ if $0 \leq x(0) < a_1$ and $\lim_{t\to\infty} x(t) = K_1$ if $x(0) > a_1$. Therefore, there exists a population level threshold a_1 below which the population becomes extinct.

Wang et al. (1999), on the other hand, use the following equation to model Allee effects for a single population N:

$$N' = N\left(b\left(1 - \frac{N}{R}\right) \cdot \frac{N}{C + N} - D\right), \tag{2.3}$$

where all of the parameters $b,\ R,\ C,\ D$ are positive with $b > D$, and C is the Allee constant. The larger C indicates the stronger Allee effects. From Equations (2.2) and (2.3), it is clear that our modelling aspect is different from that of the model considered by Wang et al. (1999).

When a population is in danger of extinction, frequently, an external population is released into the resident population to conserve the endangered population (Hobday & Tegner, 2000; Nock et al., 2011). With the equation given in (2.2), we propose the following competition model in which population x is subject to Allee effects and is also under stocking

$$\begin{aligned} x' &= r_1 x\left(1 - \frac{x}{K_1}\right)(x - a_1) - \frac{r_1 c_1 x y}{K_1} + s x, \\ y' &= r_2 y\left(1 - \frac{y}{K_2}\right) - \frac{r_2 c_2 x y}{K_2}, \end{aligned} \tag{2.4}$$

where $r_1,\ K_1,\ c_1,\ r_2,\ K_2,\ c_2$ are positive, $0 < a_1 < K_1$, and $s > 0$ is the constant proportionality of stocking. Notice that such a constant rate of stocking is also considered by Brauer and Soudack for a class of predator–prey models (Brauer & Soudack, 1982).

There are seven parameters in (2.4). We can rescale the system to reduce the number of parameters. Let

$$\hat{x} = \frac{x}{K_1},\ \hat{y} = \frac{y}{K_2}, \quad \hat{t} = r_2 t,$$

and define

$$\hat{r}_1 = \frac{r_1 K_1}{r_2},\ \hat{s}_1 = \frac{s}{r_2},\ \hat{c}_1 = \frac{r_1 c_1 K_2}{r_2 K_1},\ \hat{a}_1 = \frac{a_1}{K_1},\ \text{and } \hat{c}_2 = \frac{c_2 K_1}{K_2}.$$

Then by ignoring the hats, system (2.4) is converted to

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= r_1 x(1-x)(x-a_1) - c_1 xy + s_1 x,\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= y(1-y) - c_2 xy,\end{aligned} \tag{2.5}$$

with non-negative initial conditions. Model (2.5) has only four parameters, where $0 < a_1 < 1$ and r_1, c_1, c_2, s_1 are positive. We assume

$$s_1 > r_1 a_1, \tag{2.6}$$

so that the constant proportionality is greater than the product of a_1 and r_1. One can see that population x also exhibits Allee effects if the stocking is small, $s_1 < r_1 a_1$.

If $y(0) = 0$, then $y(t) = 0$ for $t > 0$ and (2.5) reduces to the scalar equation

$$x' = x(r_1(1-x)(x-a_1) + s_1). \tag{2.7}$$

Let $f(x)$ denote the right hand side of (2.7). Dynamics of Equation (2.7) can be easily determined. Indeed, 0 is always a steady state and Equation (2.7) has a unique positive steady state $\bar{x}$ under (2.6), where

$$\bar{x} = \frac{1+a_1}{2} + \frac{\sqrt{(1+a_1)^2 + \frac{4}{r_1}(s_1 - r_1 a_1)}}{2}. \tag{2.8}$$

If $s_1 > r_1 a_1$ is not assumed, then (2.7) may have two positive steady states, and as a result, the population will also be subject to Allee effects even with stocking. It can be readily shown that the positive steady state $\bar{x}$ is globally asymptotically stable for (2.7) on $(0, \infty)$.

We are now ready to study the full system (2.5). Clearly, solutions of (2.5) exist, remain non-negative and are bounded for $t > 0$. System (2.5) has boundary steady states $E_0 = (0, 0)$, $E_1 = (\bar{x}, 0)$ and $E_2 = (0, 1)$. Their stability depends on the Jacobian matrix J evaluated at the steady states with

$$J(E_0) = \begin{bmatrix} s_1 - r_1 a_1 & 0 \\ 0 & 1 \end{bmatrix}, \quad J(E_1) = \begin{bmatrix} f'(\bar{x}) & -c_1 \bar{x} \\ 0 & 1 - c_2 \bar{x} \end{bmatrix}, \quad \text{and } J(E_2) = \begin{bmatrix} s_1 - r_1 a_1 - c_1 & 0 \\ -c_2 & -1 \end{bmatrix}.$$

Since each of these matrices are triangular, stability of the boundary steady states is summarized below.

Proposition 2.1 *System* (2.5) *has three boundary steady states* $E_0 = (0, 0)$, $E_1 = (\bar{x}, 0)$ *and* $E_2 = (0, 1)$, *where* E_0 *is a repeller. Steady state* E_1 *is asymptotically stable if* $c_2 \bar{x} > 1$ *and a saddle point if* $c_2 \bar{x} < 1$, *and* E_2 *is asymptotically stable if* $s_1 < r_1 a_1 + c_1$ *and a saddle point if* $s_1 > r_1 a_1 + c_1$.

Notice model (2.5) is a two-dimensional competitive system with respect to the partial ordering $\leq_K$, where

$$(x, y) \leq_K (z, w) \text{ if and only if } x \leq z \text{ and } y \geq w.$$

Since solutions of (2.5) are bounded, every solution of (2.5) converges to a steady state by Smith and Waltman (1995, Appendix C) due to competitiveness. Let (x_0, y_0) in $\mathbb{R}^2_+$ be given arbitrarily. Relative to (x_0, y_0), we can separate $\mathbb{R}^2_+$ into four regions Q_i, $1 \leq i \leq 4$, in a counter-clockwise manner:

$$\begin{aligned} Q_1(x_0, y_0) &= \{(x, y) \in \mathbb{R}^2_+ : x \geq x_0, y \geq y_0\}, \\ Q_2(x_0, y_0) &= \{(x, y) \in \mathbb{R}^2_+ : x \leq x_0, y \geq y_0\}, \end{aligned} \tag{2.9}$$

and Q_3 and Q_4 are defined similarly. Then, Q_2 and Q_4 are positively invariant for (2.5) if (x_0, y_0) is a steady state. Figure 1(a) plots a point (x_0, y_0) and illustrates the four regions Q_i, $1 \leq i \leq 4$, relative to (x_0, y_0).

Interior steady states are the positive intersections of the isoclines. The non-trivial x- and y-isoclines are given by

$$q_1(x) = \frac{1}{c_1}[r_1(1-x)(x-a_1) + s_1] \text{ and } g_2(x) = 1 - c_2 x, \tag{2.10}$$

respectively. Let $h(y) = \frac{1}{c_2}(1-y)$ be the inverse function of g_2. Notice $q_1(0) = \frac{1}{c_1}(s_1 - r_1 a_1) > 0$, $q_1(\bar{x}) = 0$, and $y = q_1(x)$ is a concave down parabola with vertex at $\hat{x} = \frac{1+a_1}{2}$. We separate our discussion into the following cases:

$$\text{case 1: } c_1 < s_1 - r_1 a_1 \text{ and } 1 < c_2\bar{x}, \quad \text{case 2: } c_1 > s_1 - r_1 a_1 \text{ and } 1 < c_2\bar{x},$$

$$\text{case 3: } c_1 < s_1 - r_1 a_1 \text{ and } 1 > c_2\bar{x}, \quad \text{case 4: } c_1 > s_1 - r_1 a_1 \text{ and } 1 > c_2\bar{x},$$

where the critical case of equality in cases 1–4 is ignored since parameter values are estimates. In the following, we provide asymptotic dynamics of the model. Their proofs are presented in Appendix 1.

If case 1 holds, then from the graphs of $y = q_1(x)$ and $y = g_2(x)$, as illustrated in Figure 1(b), that there is no interior steady state. Since every solution of (2.5) converges to

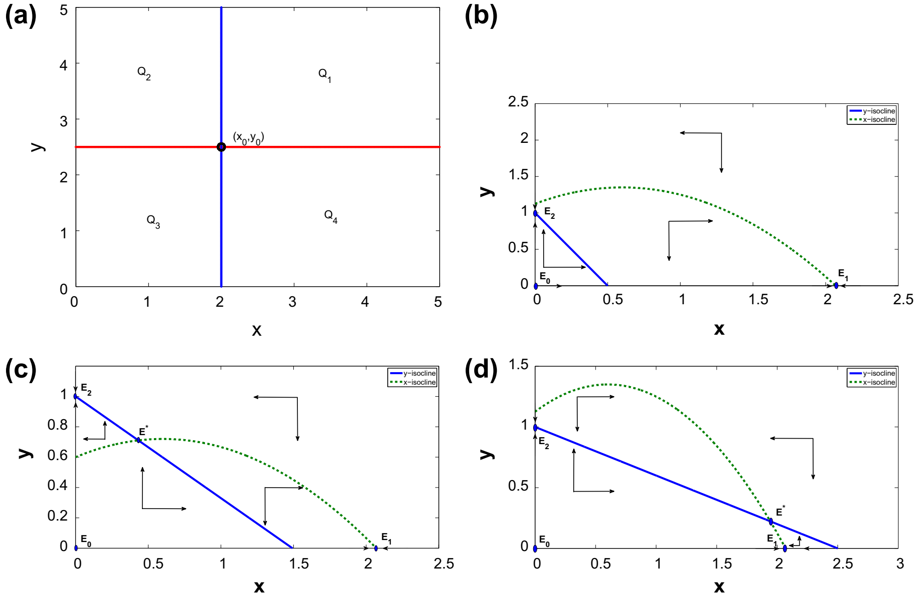

Figure 1. (a) illustrates the regions Q_1–Q_4 defined in (2.9) relative to the point (x_0, y_0). (b)–(d) are the isoclines of system (2.5) under different parameter regimes: (b) $c_1 < s_1 - r_1 a_1$ and $1 < c_2\bar{x}$, (c) $c_1 > s_1 - r_1 a_1$ and $1 < c_2\bar{x}$, and (d) $c_1 < s_1 - r_1 a_1$ and $1 > c_2\bar{x}$.

a steady state, it follows from Proposition 2.1 that $E_1 = (\bar{x}, 0)$ is globally asymptotically stable in $\mathrm{int}(\mathbb{R}^2_+)$.

Theorem 2.2 *If $c_1 < s_1 - r_1 a_1$ and $1 < c_2 \bar{x}$, then system (2.5) has no interior steady states and $E_1 = (\bar{x}, 0)$ is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}^2_+)$.

Since c_1 is small and c_2 is large under the assumption of Theorem 2.2, population x is more aggressive than the y population in competing for resources. Even though population x is subject to Allee effects, the stocking s_1 is large, so the x population drives the y population to extinction.

When case 2 occurs, then a simple graphical analysis shows that (2.5) has a unique interior steady state $E^* = (x^*, y^*)$, where $0 < y^* < 1$ and $0 < x^* < \bar{x}$. See Figure 1(c). Furthermore, $E_0 = (0, 0)$ is a repeller, and $E_1 = (\bar{x}, 0)$ and $E_2 = (0, 1)$ are asymptotically stable by Proposition 2.1. The asymptotic dynamics of the model for case 2 are summarized below.

Theorem 2.3 *Let $c_1 > s_1 - r_1 a_1$ and $1 < c_2 \bar{x}$. Then (2.5) has a unique interior steady state $E^* = (x^*, y^*)$, where E^* is a saddle point. The stable manifold of E^* separates $\mathbb{R}^2_+$ into two positively invariant regions R_1 and R_2 such that $E_2 = (0, 1)$ and $E_1 = (\bar{x}, 0)$ are globally asymptotically stable in R_1 and R_2, respectively.*

From the assumption of Theorem 2.3, both c_1 and c_2 are large but the stocking s_1 is not large, so that competition between these two populations is intense. Therefore, competitive exclusion occurs with competition outcomes depending on initial populations. The population with a larger population size will be more likely to outcompete the other population.

Consider case 3, where $c_1 < s_1 - r_1 a_1$ and $1 > c_2 \bar{x}$. A simple graphical analysis as illustrated in Figure 1(d) shows that (2.5) has a unique interior steady state $E^* = (x^*, y^*)$. Notice $E_0 = (0, 0)$ is a repeller, $E_1 = (\bar{x}, 0)$ is a saddle point with stable manifold on the positive x-axis, and $E_2 = (0, 1)$ is also a saddle point with stable manifold on the positive y-axis. We summarize the dynamical behaviour of (2.5).

Theorem 2.4 *Let $c_1 < s_1 - r_1 a_1$ and $1 > c_2 \bar{x}$. Then, (2.5) has a unique interior steady state $E^* = (x^*, y^*)$ and E^* is globally asymptotically stable in* $\mathrm{int}(\mathbb{R}^2_+)$.

Competition coefficients c_1 and c_2 are small under the assumption of Theorem 2.4, which indicates that both populations are less aggressive in competing with each other. On the other hand, stocking s_1 is large. Therefore, both populations can coexist for all positive initial populations.

When case 4 holds, i.e. $c_1 > s_1 - r_1 a_1$ and $1 > c_2 \bar{x}$, then $E_1 = (\bar{x}, 0)$ is a saddle point and $E_2 = (0, 1)$ is asymptotically stable by Proposition 2.1. Moreover, (2.5) may have either two interior steady states $E_i^* = (x_i^*, y_i^*)$, $i = 1, 2$, where $0 < x_1^* < x_2^* < \bar{x}$ and $y_2^* < y_1^* < 1$, a unique interior steady state $E^* = (x^*, y^*)$ when $y = g_2(x)$ is tangent to $y = q_1(x)$ at E^*, or no interior steady state. See Figure 2(a)–(c). We label these as cases 4(a)–4(c), respectively. Since parameter values are estimates, the probability of tangency is very small. Therefore, we do not provide the dynamics for case 4(b). The proof of Theorem 2.5 is omitted since it is similar to the proofs of Theorems 2.3 and 2.4.

Theorem 2.5 *Let $c_1 > s_1 - r_1 a_1$ and $1 > c_2 \bar{x}$. Then (2.5) may have either two, one or no interior steady states. The unique interior steady state E^* is non-hyperbolic whenever it exists. If (2.5) has two interior steady states, $E_i^*(x_i^*, y_i^*)$, $i = 1,\ 2$, $0 < x_1^* < x_2^* < \bar{x}$ and $y_2^* < y_1^* < 1$, then E_1^* is a saddle point and E_2^* is asymptotically stable. The stable*

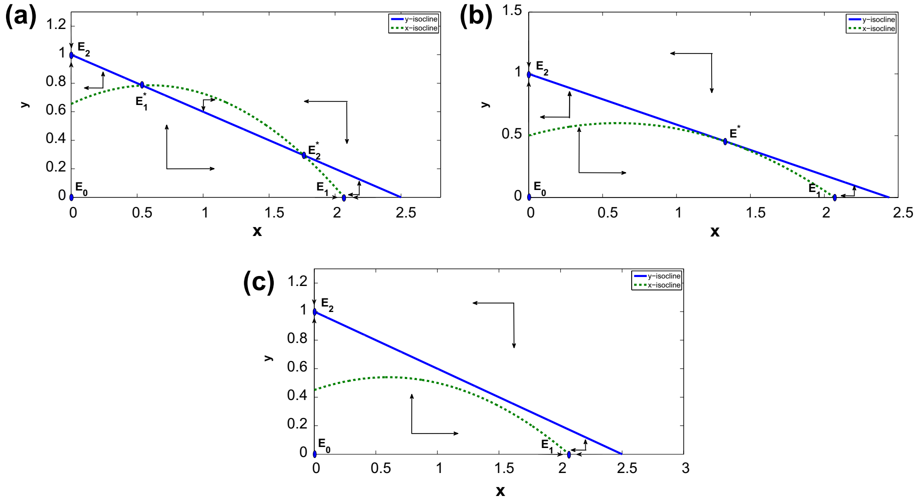

Figure 2. Isoclines of system (2.5) when $c_1 > s_1 - r_1a_1$ and $1 > c_2\bar{x}$ hold. Plots (a)–(c) correspond to the cases 4(a)–4(c), where there are two interior steady states, a unique interior steady state, and no interior steady state, respectively.

Table 1. Asymptotic dynamics of model (2.5).

Parameter regime	Interior steady states	Asymptotic dynamics
$c_1 < s_1 - r_1a_1$ and $1 < c_2\bar{x}$	None	E_1 is GAS
$c_1 > s_1 - r_1a_1$ and $1 < c_2\bar{x}$	Unique E^*	E_2 and E_1 are GAS in the respective regions
$c_1 < s_1 - r_1a_1$ and $1 > c_2\bar{x}$	Unique E^*	E^* is GAS
$c_1 > s_1 - r_1a_1$ and $1 > c_2\bar{x}$	None	E_2 is GAS
	Two with $E_1^* <<_K E_2^*$	E_2 and E_2^* are GAS in the respective regions

manifold of E_1^* *separates* $\mathbb{R}_+^2$ *into two positively invariant regions such that* E_2 *and* E_2^* *are globally asymptotically stable in the respective regions. Moreover,* $E_2 = (0, 1)$ *is globally asymptotically stable if* (2.5) *has no interior steady state.*

Under the assumption of Theorem 2.5, population y is more aggressive but population x is under stocking. The competition outcome is not clear from the given assumption since either population y dominates or both populations coexist as illustrated in Theorem 2.5. In the following, we provide sufficient conditions in terms c_1 and c_2 so that either coexistence or competitive exclusion occurs.

THEOREM 2.6 *If* (A4) *holds, then* (2.5) *has no interior steady states. If* (A6) *holds, then* (2.5) *has two interior steady states.*

There are three conditions in (A4). Two of them are those given in the assumption of Theorem 2.5, namely $c_1 > s_1 - r_1a_1$ and $1 > c_2\bar{x}$. The other condition is $c_2 < \zeta_s(c_1)$, where ζ_s is defined by (A3). This latter condition provides a direct comparison between the two competition coefficients c_1 and c_2. The condition implies that population x is less aggressive than population y. Therefore, the y population drives the x population to extinction.

There are also three inequalities listed in (A6), where two of them are the same as those presented in the assumption of Theorem 2.5. The other condition is $\zeta_s(c_1) < c_2 < \psi_s(c_1)$, with ψ_s given in (A5). We can interpret these two inequalities by saying that population x is more aggressive as compared to the previous scenario where $c_2 < \zeta_s(c_1)$. However, population x is not sufficiently aggressive since $c_2 < \psi_s(c_1)$. Therefore, coexistence of both populations is possible if the initial x population is large. Otherwise, the x population goes extinct since population y is aggressive.

The asymptotic dynamics of model (2.5) are summarized in Table 1.

3. Summary and conclusions

White abalone is an endangered species which is also subject to Allee effects (Hobday & Tegner, 2000). It is well documented that the species cannot recover naturally without stocking (Hobday & Tegner, 2000; Stierhoff et al., 2012). In Li and Jiao (2015), a size-structured single population matrix model is proposed to study the effects of stocking by different sizes of abalone. In any natural environment, however, populations are likely to interact with other populations. It is the goal of this study to investigate the impact of Allee effects and stocking on two competing populations.

If only x population is considered, then it is clear that the population can persist indefinitely for all positive population distributions if the stocking s_1 is larger than the intrinsic growth rate and the Allee threshold of the x population. However, competition with another population may change its survival as demonstrated in the present study. In some cases, the endangered population can drive the other population to extinction while in other cases the endangered population cannot survive even with the man-made control strategy.

If population x is aggressive and the stocking is large, then such a control strategy will drive the other population to extinction. Therefore, this prevention scheme is not ideal in terms of biodiversity. On the other hand, if population y is more aggressive than the x population and the stocking is small, then the y population will drive the x population to extinction and such a control strategy cannot preserve the endangered population. The other cases derived from this study can be interpreted similarly. The best stocking strategy is given by case 3, where both populations are not aggressive but the stocking is large. In such case, both populations can persist indefinitely as a coexisting steady state.

Our investigation provides asymptotic dynamics of two competing populations where one population is subject to Allee effects and is also under stocking. The success of this mandated implanting strategy depends not only on the stocking size but also on the nature of the two interacting species. The degree of intensity of the competition between these two populations plays an important role in determining competing outcomes and population coexistence. We conclude that considerable care must be taken before implanting the population that is subject to Allee effects.

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References

Allee, W. C. (1938). *The social life of animals*. London: William Heinemann.

Allen, L., Fagan, J., Hognas, G., & Fagerholm, H. (2005). Population extinction in discrete-time stochastic population models with an Allee effect. *Journal of Difference Equations and Applications, 11*, 273–293.

Allen, L. J. S. (2006). *An introduction to mathematical biology*. Upper Saddle River, NJ: Prentice-Hall.

AlSharawi, Z., & Rhouma, M. (2009). Coexistence and extinction in a competitive exclusion Leslie/Gower model with harvesting and stocking. *Journal of Difference Equations and Applications, 15*, 1031–1053.

Amarasekare, P. (1998). Allee effects in metapopulation dynamics. *The American Naturalist, 152*, 298–302.

Begon, M., Harper, J., & Townsend, C. (1996). *Ecology: Individuals, populations and communities*. New York, NY: Blackwell.

Brauer, F., & Soudack, A. C. (1982). On constant effort harvesting and stocking in a class of predator-prey systems. *Journal of Theoretical Biology, 95*, 247–252.

Chow, Y., & Jang, S. R.-J. (2014). Multiple attractors in a Leslie–Gower competition system with Allee effects. *Journal of Difference Equations and Applications, 20*, 169–187.

Chow, Y., & Jang, S. R.-J. (2015). Asymptotic dynamics of the Leslie–Gower competition system with Allee effects and stocking. *Advances in Difference Equations, 2015*(1), 1–19.

Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee effects in ecology and conservation*. New York, NY: Oxford University Press.

Cushing, J. M. (1988). The Allee effect in age-structured population dynamics. In T. Hallam, L. Gross, & S. Levin (Eds.), *Mathematical ecology* (pp. 479–505). New York, NY: Springer-Verlag.

Dennis, B. (2002). Allee effects in stochastic populations. *Oikos, 96*, 389–401.

Elaydi, S., & Yakubu, A. (2002). Global stability of cycles: Lotka-Volterra competition model with stocking. *Journal of Difference Equations and Applications, 8*, 537–549.

Hilker, F. M. (2010). Population collapse to extinction: The catastrophic combination of parasitism and Allee effect. *Journal of Biological Dynamics, 4*, 86–101.

Hobday, A. J., & Tegner, M. J. (2000). *Status review of White abalone (Haliotis sorenseni) throughout its Range in California and Mexico*. Long Beach, CA: US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Region Office.

Kang, Y. (2013). Scramble competitions can rescue endangered species subject to strong Allee effects. *Mathematical Biosciences, 241*, 75–87.

Keitt, T., Lewis, M., & Holt, R. (2001). Allee effects, invasion pinning, and species borders. *The American Naturalist, 157*, 203–216.

Kulenović, M., & Nurkanović, M. (2012). Global behavior of a two-dimensional competitive system of difference equations with stocking. *Mathematical and Computer Modelling, 55*, 1998–2011.

Lawrence, P. (2001). *Differential equations and dynamical systems*, Vol. 74. New York, NY: Springer-Verlag.

Li, Y., & Jiao, Y. (2015). Evaluation of stocking strategies for endangered white abalone using a hierarchical demographic model. *Ecological Modelling, 299*, 14–22.

Livadiotis, G., & Elaydi, S. (2012). General Allee effect in two-species population biology. *Journal of Biological Dynamics, 6*, 959–973.

Morozov, A., Petrovskii, S., & Li, B.-L. (2004). Bifurcations and chaos in a predator-prey system with the Allee effect. *Proceedings of the Royal Society of London Series B, 271*, 1407–1414.

Nock, C., Ovenden, J., Butler, G., Wooden, I., Moore, A., & Baverstock, J. (2011). Population structure, effective population size and adverse effects of stocking in the endangered Australian eastern freshwater cod Maccullochella ikei. *Journal of Fish Biology, 78*, 303–321.

Smith, H., & Waltman, P. (1995). *The theory of the chemostat*. New York, NY: Cambridge University Press.

Stierhoff, K. L., Neuman, M., & Butler, J. L. (2012). On the road to extinction? Population declines of the endangered white abalone, *Haliotis sorenseni*. *Biological Conservation, 152*, 46–52.

Thieme, H. R., Dhirasakdanon, T., Han, Z., & Trevino, R. (2009). Species decline and extinction: Synergy of infectious diseases and Allee effect. *Journal of Biological Dynamics, 3*, 305–323.

Voorn, G., Hemerik, L., Boer, M., & Kooi, B. (2007). Heteroclinic orbits indicate overexploitation in predator-prey systems with a strong Allee effect. *Mathematical Biosciences, 209*, 451–469.

Wang, G., Liang, X.-G., & Wang, F.-Z. (1999). The competitive dynamics of populations subject to an Allee effect. *Ecological Modelling, 124*, 183–192.

Zhou, S., Liu, Y., & Wang, G. (2005). The stability of predator-prey systems subject to the Allee effects. *Theoretical Population Biology, 67*, 23–31.

Zhou, S., & Wang, G. (2004). Allee-like effects in meta population dynamics. *Mathematical Biosciences, 189*, 103–113.

Appendix 1

Proof of Theorem 2.3 We prove that E^* is a saddle point. To this end, the Jacobian matrix J evaluated at E^* is given by

$$J(E^*) = \begin{bmatrix} \dfrac{\partial f_1}{\partial x} & \dfrac{\partial f_1}{\partial y} \\ \dfrac{\partial f_2}{\partial x} & \dfrac{\partial f_2}{\partial y} \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix},$$

where $\dfrac{\partial f_1}{\partial y} < 0$, $\dfrac{\partial f_2}{\partial x} < 0$, and $\dfrac{\partial f_2}{\partial y} < 0$. The characteristic equation of $J(E^*)$ is $\lambda^2 - (a+d)\lambda + (ad - bc) = 0$ with discriminant $\Delta = (a-d)^2 + 4bc > 0$. Therefore, eigenvalues of $J(E^*)$ are real numbers. Moreover, $f_1(x, q_1(x)) = 0$ and $f_2(h(y), y) = 0$ imply $\dfrac{\partial f_1}{\partial x} + \dfrac{\partial f_1}{\partial y} q_1'(x) = 0$ and $\dfrac{\partial f_2}{\partial x} h'(y) + \dfrac{\partial f_2}{\partial y} = 0$ respectively. Therefore, it can easily be shown that

$$ad - bc = \frac{\partial f_1}{\partial y}\frac{\partial f_2}{\partial x}(q_1'(x^*)h'(y^*) - 1). \tag{A1}$$

Observe that $q_1'(x^*) > g_2'(x^*)$, where $g_2'(x^*) = \dfrac{1}{h'(y^*)}$, and hence $ad - bc < 0$ by (A1). Therefore, one eigenvalue λ_- of $J(E^*)$ is negative and the other eigenvalue λ_+ is positive and hence E^* is a saddle point. An eigenvector $(v_1, v_2)^T$ of $J(E^*)$ belonging to λ_- can be chosen to be $v_1 = 1$ and $v_2 = -\dfrac{a - \lambda_-}{b} > 0$ since $b < 0$ and $\lambda_- < 0$. Thus, the stable manifold M^+ of E^* is in $Q_1(E^*) \bigcup Q_3(E^*)$. Since $Q_1(E^*)$ has no steady state, M^+ is unbounded in $Q_1(E^*)$ by the existence and uniqueness theorem of the initial value problems (Lawrence, 2001). Also, solutions on the non-negative x and y axes converge to $E_1 = (\bar{x}, 0)$ and to $E_2 = (0, 1)$ respectively. Therefore, M^+ has an endpoint at $E_0 = (0, 0)$. It follows that M^+ separates $\mathbb{R}_+^2$ into two positively invariant regions R_1 and R_2 with $E_2 \in R_1$ and $E_1 \in R_2$, and the result follows. □

Proof of Theorem 2.4 It is enough to prove that E^* is asymptotically stable. Indeed, since $1 < q_1(0)$ and $y = g_2(x)$ is strictly decreasing, $y = q_1(x)$ and $y = g_2(x)$ must intersect at a point (x^*, y^*) for which $q_1'(x^*) < 0$. Hence $a = \dfrac{\partial f_1}{\partial x} = r_1 x^*(1 - 2x^* + a_1) < 0$. Since $g_2'(x^*) > q_1'(x^*)$ implies $1 < q_1'(x^*)h'(y^*)$, there holds $ad - bc > 0$ by (A1). Also, $a < 0$ and $d < 0$. Thus both eigenvalues of $J(E^*)$ are negative and E^* is asymptotically stable. □

Proof of Theorem 2.6 Let $c_1 > s_1 - r_1 a_1$ and $1 > c_2\bar{x}$. We derive sufficient conditions for which (2.5) has either no interior steady state or two interior steady states. Setting the two isoclines equal, $q_1(x) = g_2(x)$, one obtains

$$r_1 x^2 - (r_1(1 + a_1) + c_1 c_2)x + c_1 + r_1 a_1 - s_1 = 0. \tag{A2}$$

Let $R(x)$ denote the left hand side of (A2). Then, any positive solution x^* of $R(x) = 0$ results in an interior steady state if and only if $c_2 x^* < 1$. By the assumption $c_1 > s_1 - r_1 a_1$ and $c_2\bar{x} < 1$,

$R(x) = 0$ may have either one, two or no positive solutions

$$x_{\pm}^{s} = \frac{c_1c_2 + r_1(1+a_1) \pm \sqrt{[c_1c_2 + r_1(1+a_1)]^2 - 4r_1(c_1 + r_1a_1 - s_1)}}{2r_1},$$

depending on the magnitude of $[c_1c_2 + r_1(1+a_1)]^2 - 4r_1(c_1 + r_1a_1 - s_1)$ along with whether $c_2x_{\pm}^{s} < 1$.

If $[c_1c_2 + r_1(1+a_1)]^2 < 4r_1(c_1 + r_1a_1 - s_1)$, then $x_{\pm}^{s}$ are complex numbers and thus (2.5) has no interior steady states. This inequality can be shown to be equivalent to $c_2 < \zeta_s(c_1)$, where

$$\zeta_s(c_1) := \frac{2\sqrt{r_1(c_1 + r_1a_1 - s_1)} - r_1(1+a_1)}{c_1}, \; c_1 > s_1 - r_1a_1. \tag{A3}$$

A straightforward calculation shows that $\zeta_s(c_1)$ is strictly increasing on $(s_1 - r_1a_1,\ c_{s1}^{*})$ and strictly decreasing on $(c_{s1}^{*},\ \infty)$, where $c_{s1}^{*} = r_1\bar{x}^2 + s_1 - r_1a_1$. Consequently, a set of sufficient conditions for which (2.5) has no interior steady state is given by

$$c_2\bar{x} < 1,\; c_2 < \zeta_s(c_1),\; c_1 > s_1 - r_1a_1. \tag{A4}$$

Since $1 < c_2\bar{x}$ and $x_{+}^{s} < \bar{x}$ imply $c_2x_{+}^{s} < 1$, a set of sufficient conditions for the existence of two interior steady states is therefore given by $1 < c_2\bar{x},\ c_2 > \zeta_s(c_1),\ c_1 > s_1 - r_1a_1,$ and $x_{+}^{s} < \bar{x}$. Furthermore, $x_{+}^{s} < \bar{x}$ is equivalent to

$$r_1(1+a_1) + c_1c_2 + \sqrt{[r_1(1+a_1) + c_1c_2]^2 - 4r_1(c_1 + r_1a_1 - s_1)} < 2r_1\bar{x}.$$

We set

$$r_1(1+a_1) + c_1c_2 + \sqrt{[r_1(1+a_1) + c_1c_2]^2} < 2r_1\bar{x},\ \text{or equivalently},\ c_2 < \frac{r_1(\bar{x} - 1 - a_1)}{c_1}.$$

Denote

$$\psi_s(c_1) := \frac{r_1(\bar{x} - 1 - a_1)}{c_1},\; c_1 > s_1 - r_1a_1. \tag{A5}$$

Then a set of sufficient conditions for the existence of two interior steady states is

$$c_2\bar{x} < 1,\; \zeta_s(c_1) < c_2 < \psi_s(c_1),\; c_1 > s_1 - r_1a_1. \tag{A6}$$

□