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ON THE DYNAMICS OF EVOLUTIONARY COMPETITION MODELS

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ABSTRACT. As exemplified by classic Lotka–Volterra theory, there are several canonical outcomes possible to a two species (interference) competitive interaction: coexistence, initial condition-dependent competitive exclusion of one species, or the global exclusion of one species. Evolutionary versions of Lotka–Volterra dynamics have been investigated in order to see the role that evolutionary adaptation can play in influencing the competitive outcome. For the most part, however, these investigations have been carried out by numerical simulations. In this paper, we provide some rigorous mathematical criteria concerning the outcome of a competition between two species x_1 and x_2 when evolution is taken into account. Motivated by two classic experiments in which the outcome of two competing beetle species was observed to change due to phenotypic or genetic changes in one species, we consider the case when only the species x_2 can evolutionarily adapt. Using methods from persistence theory, we obtain criteria under which x_2 will persist and criteria under which x_1 will persist.

KEY WORDS: Competition dynamics, Leslie–Gower model, evolution, evolutionary game theory, persistence.

1. Introduction.

The (discrete-time) Leslie–Gower model for two competing species

$$x_1(t+1) = x_1(t)\frac{e^r}{1 + c_{11}x_1 + c_{12}x_2} \tag{1a}$$

$$x_2(t+1) = x_2(t)\frac{e^r}{1 + c_{21}x_1 + c_{22}x_2} \tag{1b}$$

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with $r > 0$, $c_{ij} \geq 0$, and $c_{ii} > 0$ has the same (global) asymptotic dynamic alternatives as the classic (continuous time) Lotka–Volterra competition model. Namely, the (open) positive cone $\mathbb{R}_2^+$ of the (x_1, x_2)-plane is forward invariant and all solutions $(x_1(t), x_2(t))$ in $\mathbb{R}_2^+$ satisfy one of the following alternatives (Smith [1998]; Cushing et al. [2004]; Kulenović and Merino [2006]).

(I) $\lim_{t\to+\infty}(x_1(t), x_2(t)) = (K_1, 0)$ or $(0, K_2)$ except for the stable manifold of the saddle equilibrium $(\bar{x}_1, \bar{x}_2) \in R_2^+$;
(II) $\lim_{t\to+\infty}(x_1(t), x_2(t)) = (K_1, 0)$ where $K_1 = (e^r - 1)/c_{11}$;
(III) $\lim_{t\to+\infty}(x_1(t), x_2(t)) = (\bar{x}_1, \bar{x}_2) \in R_2^+$, a stable equilibrium;
(IV) $\lim_{t\to+\infty}(x_1(t), x_2(t)) = (0, K_2)$ where $K_2 = (e^r - 1)/c_{22}$.

Alternatives II and IV imply global competitive exclusion in the sense that one or the other species survives while the other goes extinct. The same is true (generically) of alternative I except that which species is competitively eliminated is initial condition dependent. Alternative III implies competitive coexistence. Which competitive outcome occurs depends on the coefficients c_{ij}. Specifically, conditions for each alternative to occur are

(I) $c_{12} - c_{22} > 0$, $c_{21} - c_{11} > 0$;
(II) $c_{12} - c_{22} < 0$, $c_{21} - c_{11} > 0$;
(III) $c_{12} - c_{22} < 0$, $c_{21} - c_{11} < 0$;
(IV) $c_{12} - c_{22} > 0$, $c_{21} - c_{11} < 0$.

These alternatives can be conveniently summarized by the location of the point P with coordinates $(c_{12} - c_{22}, c_{21} - c_{11})$ in the Cartesian plane $\mathbb{R}^2$ shown in Figure 1. We refer to this plane as the *competitive outcome plane*. If the competitive coefficients c_{ij} are fixed in time, then one can determine the competitive outcome predicted by (1) from the quadrant in which P lies. If the coefficients are altered, then the competitive outcome will be altered according to the new location of the point P in the competitive outcome plane. In this way, one can determine if a change in competitive outcome might occur because of changes in the competitive coefficients c_{ij} and hence the location of P.

There are many reasons why the coefficients c_{ij} might change (stochasticity, seasonal periodicity, environmental perturbations, etc.). One way is through evolutionary adaptations due to Darwinian principles. This latter case was considered in Rael et al. [2011] by means of an evolutionary game theoretic version of (1). That study was motivated by the results of two exceptional experiments, both of historical importance with regard to the development of competition theory, conducted with species of the insects *Tribolium* (flour beetles). In those experiments, expected competitive outcomes (based on extensive past experiments) changed in cultures in which genetically controlled behavioral changes were also noted. In one of these

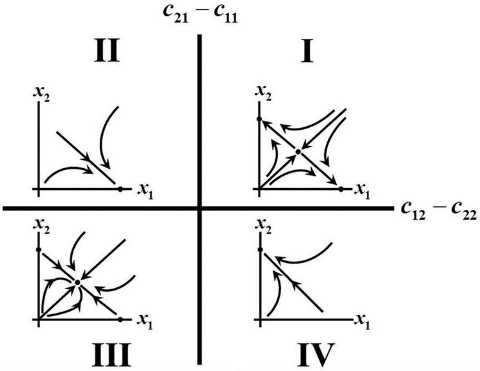

FIGURE 1. The outcomes of the Leslie–Gower competition model (1) are determined by the location of the point P in this competitive outcome plane, as seen represented by phase plane portraits.

experiments, the change in competitive outcome corresponded to a move of the point P from quadrant II to IV (a competitive reversal) (Dawson [1967, 1969]). In the other experiments, the change in competitive outcome corresponded to a move from quadrant I to IV (from exclusion to coexistence) (Park et al. [1964]; Leslie et al. [1968]). While some equilibrium and local stability analysis was performed in Rael et al. [2011], most of the study was based on extensive numerical simulations of the evolutionary model.

In this paper, we consider the same evolutionary version of the model (1) studied in Rael et al. [2011] and give rigorous mathematical proofs of some of the observations and conclusions made in that paper. We focus solely on the first of the experimental backdrops studied in Rael et al. [2011], namely the case when only one of the two species, namely, x_2 is subject to evolutionary adaptations. We will study two scenarios. In the first scenario, we establish conditions under which x_2 will no longer go extinct if it is allowed to evolutionarily adapt (Theorems 1 and 2). In the second scenario, we shift our attention to species x_1 and establish conditions under which it will not be forced to extinction by an evolutionarily adapting competitor x_2 (Theorem 3). Formal proofs of the theorems appear in the Appendix.

2. A Leslie–Gower evolutionary competition model. For $i = 1, 2$, we let x_i denote the density of species i and u_i denote the mean of the phenotypic traits of species i. Here $u_i \in \mathbb{R}$, the set of evolutionarily feasible traits. Let σ_i^2 denote the variance in traits present in species x_i about the mean trait u_i (Vincent and Brown [2005]). We consider the following evolutionary game theoretic version of the Leslie–Gower competition model (1) studied in Rael et al. [2011] (also see Vincent and Brown [2005]):

$$x_1(t+1) = x_1(t)\ G(v, u_1(t), u_2(t), x_1(t), x_2(t))|_{v=u_1(t)} \tag{2a}$$

$$x_2(t+1) = x_2(t)\, G(v, u_1(t), u_2(t), x_1(t), x_2(t))|_{v=u_2(t)} \tag{2b}$$

$$u_1(t+1) = u_1(t) + \sigma_1^2\, \frac{\partial \ln G(v, u_1(t), u_2(t), x_1(t), x_2(t))}{\partial v}\bigg|_{v=u_1(t)} \tag{2c}$$

$$u_2(t+1) = u_2(t) + \sigma_2^2\, \frac{\partial \ln G(v, u_1(t), u_2(t), x_1(t), x_2(t))}{\partial v}\bigg|_{v=u_2(t)} \tag{2d}$$

where

$$G(v, u_1, u_2, x_1, x_2) := \frac{e^r}{1 + c(v, u_1)x_1 + c(v, u_2)x_2} \tag{3}$$

is the *fitness-generating function* (see Vincent and Brown [2005]; Rael et al. [2011]). Here we let

$$c(v, u_j) = (e^r - 1)\frac{\alpha(v - u_j)}{K(v)} \tag{4}$$

with

$$\alpha(v - u_j) = \exp\left(-\frac{(v - u_j)^2}{2\sigma_\alpha^2}\right) \tag{5a}$$

$$K(v) = K_m \exp\left(-\frac{v^2}{2\sigma_K^2}\right). \tag{5b}$$

Note that $\alpha(u_i, u_i) = 1$ and hence $K(u_i)$ is the equilibrium level of species i in the absence of species j, and $\alpha(u_i, u_j)$ measures the competitive effects that individuals of species $j \neq i$ using strategy u_j have on the fitness of individuals of species i using strategy u_i (for more details on the interpretation of these parameters, we refer the reader to Rael et al. [2011]). Clearly, since $u_i(t)$ may vary with t, the competition coefficients $c(u_i(t), u_j(t))$ may also vary with t.

Observe that $\mathbb{R}_+^2 \times \mathbb{R}^2$ is invariant under the map (2a). We are interested in the possibility that the outcome of the competitive interaction will change due to evolutionary adaptation. Geometrically, does the evolutionary path of the (time-dependent) point

$$P(t) = (c(u_1(t), u_2(t)) - c(u_2(t), u_2(t)), c(u_2(t), u_1(t)) - c(u_1(t), u_1(t)))$$

move from its initial location

$$P(0) = (c(u_1(0), u_2(0)) - c(u_2(0), u_2(0)), c(u_2(0), u_1(0)) - c(u_1(0), u_1(0)))$$

in the competitive outcome plane to a different quadrant? In this paper, we will consider only the case when one species evolutionarily adapts, which we choose without loss in generality to be species x_2. Thus, we assume

$$\sigma_1^2 = 0. \tag{6}$$

Under the assumption (6), the mean trait

$$u_1(t) \equiv u_1 \in \mathbb{R} \text{ for all } t.$$

In this case the equations (2) reduce to the three-dimensional system

$$x_1(t+1) = x_1(t) G(u_1, u_1, u_2(t), x_1(t), x_2(t)) \tag{7a}$$

$$x_2(t+1) = x_2(t)\, G(v, u_1, u_2(t), x_1(t), x_2(t))|_{v=u_2(t)} \tag{7b}$$

$$u_2(t+1) = u_2(t) + \sigma_2^2 \left. \frac{\partial \ln G(v, u_1, u_2(t), x_1(t), x_2(t))}{\partial v} \right|_{v=u_2(t)} \tag{7c}$$

for the triple $(x_1(t), x_2(t), u_2(t))$ of dynamic state variables.

We will address two questions in this paper. First, under what conditions will x_2 persist? Of particular interest, in this case, is the scenario in which x_2 would be competitively eliminated by x_1 in the absence of evolutionary adaptation. We will establish criteria under which x_2 will not go extinct when able to adapt. A second question concerns the fate of x_1. When will it persist when confronted by an adaptive species x_2?

Our first theorem takes up the first question and provides conditions sufficient for x_2 to avoid extinction. (Proofs of all theorems appear in the Appendix.)

Theorem 1. *Assume $\sigma_\alpha^2 > \sigma_K^2$. If either*

$$\text{(i)} \quad \sigma_2^2 \leq 2 \frac{\sigma_\alpha^2 \sigma_K^2}{\sigma_\alpha^2 - \sigma_K^2}$$

or

$$\text{(ii)}\quad \sigma_2^2 > 2\frac{\sigma_\alpha^2\sigma_K^2}{\sigma_\alpha^2-\sigma_K^2}\frac{e^r}{e^r-1}$$

then

$$\liminf_{t\to+\infty}\ x_2(t) > 0$$

for every forward bounded solution $(x_1(t), x_2(t), u_2(t))$ *of (7) with initial conditions* $(x_1(0), x_2(0), u_2(0))$ *satisfying* $x_1(0) \geq 0$ *and* $x_2(0) > 0$*.*

In Theorem 1 the sustainable level of species $x_2(t)$, that is, $\liminf_{t\to\infty} x_2(t)$, will in general depend on the initial condition of the solution and, in particular, on the initial mean trait $u_2(0)$ of the species. A stronger assertion is that there is a uniform lower bound for $x_2(t)$ valid for all initial conditions. Our next theorem does this by providing conditions sufficient for uniform persistence.

Theorem 2. *Assume* $\sigma_\alpha^2 > \sigma_K^2$ *and* $\sigma_2^2 < 2\sigma_K^2$*. There exists a compact set that attracts all solutions* $(x_1(t), x_2(t), u_2(t))$ *of (7) with initial conditions* $(x_1(0), x_2(0), u_2(0))$ *satisfying* $x_1(0) \geq 0$ *and* $x_2(0) \geq 0$*. Furthermore, there exists an* $\varepsilon > 0$ *such that*

$$\liminf_{t\to\infty}\ x_2(t) > \varepsilon$$

for every solution $(x_1(t), x_2(t), u_2(t))$ *of (7) with initial conditions* $(x_1(0), x_2(0), u_2(0))$ *satisfying* $x_1(0) \geq 0$ *and* $x_2(0) > 0$*.*

The following theorem takes up the second question above: under what conditions can x_1 avoid being competitively excluded by an evolutionary adaptive species x_2?

Theorem 3. *Assume* $\sigma_\alpha^2 < \sigma_K^2$*, and* $\sigma_2^2 < 2\sigma_K^2$*. Then* $\liminf_{t\to\infty} x_1(t) > 0$ *for every bounded solution* $(x_1(t), x_2(t), u_2(t))$ *of (7) with* $x_1(0) > 0$*.*

Theorems 1 and 2 concerning the persistence of x_2 both require $\sigma_\alpha^2 > \sigma_K^2$. This means the effects of intraspecies competition, as measured by $K(v)$, are narrowly distributed with respect to the trait v (in comparison with distribution of interspecific competition effects) around the species means. In this sense the criteria given in Theorems 1 and 2, sufficient to guarantee an evolutionary reversal for species x_2 from competitive exclusion to survival, require a sufficient amount of interspecific competition between x_2 and x_1 (in comparison to intraspecific competition). In addition to this requirement, Theorems 1(i) and 2 concerning the persistence of x_2 require the speed of evolution σ_2^2 be sufficiently slow. This is in contrast to Theorem

1(ii), which requires that the speed of evolution be sufficiently fast. We conjecture that Theorem 1 remains valid when both constraints (i) and (ii) on the speed of evolution are dropped, although we were unable to prove this.

Theorem 3 makes the opposite assumption concerning competition between the species. The inequality $\sigma_\alpha^2 < \sigma_K^2$ means that the effects of intraspecific competition are more broadly trait distributed throughout the species than the effects of interspecific competition. Under this assumption, together with the speed of evolution being not too fast, Theorem 3 implies species x_1 will not be competitively eliminated by the evolving species x_2.

3. Concluding remarks. Theorems 1, 2, and 3 provide criteria under which one of species modeled by the evolutionary game theoretic version of the classic Leslie–Gower (discrete Lotka–Volterra) competition model asymptotically persists under the assumption that only one species is subject to evolutionary adaptation. These theorems provide mathematically rigorous justification for some of the results obtained in Rael et al. [2011] through numerical simulations. Although that study also included investigations in which both species were subject to evolutionary adaptation, in one of the two motivating experimental outcomes, in which competitive outcomes were reversed by an adaptive event, only one species underwent a genetic change (Dawson [1969]). Our results here address that case, but one might conjecture that they remain valid if the other species (in this case x_1) were subject to a relatively slow rate of evolution (i.e., for $\sigma_1^2 \gtrapprox 0$). It would be of interest to obtain persistence results when both species are subject to evolution.

Another open problem is to obtain criteria for the persistence of both species. All our theorems deal with the persistence of only one of the two species. Moreover, when combined, the criteria are exclusive and hence the set of theorems combined do not provide criteria for the persistence of both species. New theorems that give criteria for the evolution to coexistence and ecological diversity would be of interest. Other changes in the competitive outcome, not considered here, are also possible (as represented by evolutionary paths of the point P between different quadrants in the outcome plane in Figure 1). These also provide open questions concerning the evolutionary model (2).

Finally, we point out that *evolutionary suicide*, an evolutionary process where a viable species adapts in such a way that it can no longer persist, has been extensively studied in the literature (e.g., Matsuda and Abrams [1994a], Matsuda and Abrams [1994b]; Gyllenberg and Parvinen [2001]; Parvinen et al. [2007]). In Gyllenberg et al. [2002], the authors showed that evolutionary suicide is possible in a structured metapopulation model. This motivated the question of whether it is necessary to have a structured model to observe suicide. In Gyllenberg and Parvinen [2001], they showed that this is not the case and that in an asymmetric competition model with an Allee effect, suicide can indeed occur. Furthermore, a structured model does not guarantee the possibility of evolutionary suicide as they also proved in that paper that in age-structured models of Gurtin–MacCamy type suicide cannot occur. Our results in Theorems 1 and 2 supplement these investigations as they provide conditions that guarantee that no evolutionary suicide can occur for the adapting species x_2 in the model (7).

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APPENDIX A: PRELIMINARIES

In this section, we provide some preliminaries needed to prove the theorems. To understand when $\liminf_{t\to\infty} x_2(t) > 0$, as it is customary in persistence theory we need to understand the boundary dynamics (i.e., the dynamics on the invariant set where one species is not present). In particular, to understand if x_2 persists we need to set $x_2 = 0$ and study the boundary dynamics of the invariant set $\{(x_1, x_2, u_1, u_2) \mid x_2 = 0\}$) on which species x_2 is absent. The mathematical effect of (6) is to make feasible the analysis of these boundary dynamics.

To this end, by letting $x_2(t) = 0$ for all $t \geq 0$ in (7) we obtain the following system:

$$x_1(t+1) = x_1(t)\frac{e^r}{1 + c(u_1, u_1)x_1(t)} \tag{A1a}$$

$$u_2(t+1) = u_2(t) - \sigma_2^2 \frac{c_v(u_2(t), u_1)x_1(t)}{1 + c(u_2(t), u_1)x_1(t)}, \tag{A1b}$$

where $c_v(v, u)$ denotes the partial derivative of $c(v, u)$ with respect to v. From these equations it is clear that

$$\lim_{t\to+\infty} x_1(t) = K_1 := \frac{e^r - 1}{c(u_1, u_1)}.$$

To understand the boundary dynamics and to prove persistence of x_2, it is useful to first understand the behavior (A1a) on the invariant set $\{(x_1, u_2)|x_1 = K_1\}$. Note that on this invariant set the component u_2 of any solution of (A1a) satisfies

$$u_2(t+1) = u_2(t) - \sigma_2^2 \frac{c_v(u_2(t), u_1)K_1}{1 + c(u_2(t), u_1)K_1}. \tag{A2}$$

Let

$$\beta(u) := \frac{1}{2}\left(\frac{u^2}{\sigma_K^2} - \frac{(u-u_1)^2}{\sigma_\alpha^2}\right).$$

Let $'$ denote differentiation with respect to u. Since $c_v(\, u_2, u_1) = \beta'(u_2)e^{\beta(u_2)}$, the unique equilibrium point of (A2) is

$$\bar{u} = -u_1 \frac{\sigma_K^2}{\sigma_\alpha^2 - \sigma_K^2}. \tag{A3}$$

Let

$$c_m := \frac{K_m}{e^r - 1}$$

and denote the map given by the right-hand side in (A2) by $g(u)$. With this notation, we have

$$g(u) := u - \sigma_2^2 K_1 \frac{\beta'(u)}{c_m\, e^{-\beta(u)} + K_1}\ . \tag{A4}$$

First, we perform analysis to understand the dynamics of equation (A2). To this end define

$$\sigma := \frac{1}{\sigma_K^2} - \frac{1}{\sigma_\alpha^2}.$$

For the rest of this section we assume that $\sigma > 0$.

Note that

$$g'(u) = 1 - \sigma_2^2 K_1 \left(\frac{\sigma}{c_m\, e^{-\beta(u)} + K_1} + c_m \frac{\left(\beta'\,(u)\right)^2 e^{-\beta(u)}}{(c_m\, e^{-\beta(u)} + K_1)^2}\right), \tag{A5}$$

$$g''(u) = -\frac{\sigma_2^2 K_1 c_m\, e^{-\beta(u)}\beta'(u)}{(c_m\, e^{-\beta(u)} + K_1)^2}\left(3\sigma + \left(\beta'\,(u)\right)^2 \frac{c_m\, e^{-\beta(u)} - K_1}{c_m\, e^{-\beta(u)} + K_1}\right). \tag{A6}$$

Let

$$p(u) := \frac{c_m\, e^{-\beta(u)} - K_1}{c_m\, e^{-\beta(u)} + K_1}.$$

A calculation shows

$$\text{(A7)}\qquad \frac{d}{du}[(\beta'(u))^2 p(u)] = \beta'(u)\left(2\sigma p(u) - (\beta'(u))^2 \frac{2K_1 c_m e^{-\beta(u)}}{(c_m e^{-\beta(u)} + K_1)^2}\right).$$

Note that

(i) $(\beta'(u))^2 p(\bar{u}) = 0$ and $\lim_{u\to\pm\infty}(\beta'(u))^2 p(u) = -\infty$.
(ii) If $(\beta'(u))^2 p(u) < 0$ and $u < \bar{u}$ then from (A7) it follows that $\frac{d}{du}((\beta'(u))^2 p(u)) > 0$. Thus, for $u < \bar{u}$ and as long as $(\beta'(u))^2 p(u) < 0$, then $(\beta'(u))^2 p(u)$ is increasing.
(iii) If $(\beta'(u))^2 p(u) < 0$ and $u > \bar{u}$ then from (A7) it follows that $\frac{d}{du}((\beta'(u))^2 p(u)) < 0$. Thus, for $u > \bar{u}$ and as long as $(\beta'(u))^2 p(u) < 0$, then $(\beta'(u))^2 p(u)$ is decreasing.

From (i) and (ii) it follows that there exists a $\xi \le \bar{u}$ such that $(\beta'(\xi))^2 p(\xi) = 0$ and $(\beta'(u))^2 p(u) < 0$ for $u \in (-\infty, \xi)$. Similarly, from (i) and (iii) it follows that there exists a $\eta \ge \bar{u}$ such that $(\beta'(\eta))^2 p(\eta) = 0$ and $(\beta'(u))^2 p(u) < 0$ for $u \in (\eta, \infty)$. If $\xi < \bar{u}$ then it is easily argued that $(\beta'(u))^2 p(u) \ge 0$ on $(\xi, \bar{u})$. Similarly, if $\eta > \bar{u}$ then it is easily seen that $(\beta'(u))^2 p(u) \ge 0$ on $(\bar{u}, \eta)$. Thus, considering (A6), it is clear that solving $g''(u) = 0$ is equivalent to solving

$$\text{(A8)}\qquad \beta'(u) = 0 \text{ or } (\beta'(u))^2 p(u) = -3\sigma.$$

The first equation has a unique solution at $u = \bar{u}$ and from the above discussion, we see there exist two values v and w, $v < \bar{u} < w$ such that the second equation in (A8) holds. Therefore, $g''(v) = g''(w) = g''(\bar{u}) = 0$ and g is concave down in $(-\infty, v) \cup (\bar{u}, w)$, and concave up in $(v, \bar{u}) \cup (w, \infty)$.

We will need the following lemma. It eliminates the possibility that (A2) has periodic solutions, under certain conditions. Note that

$$\sigma^{-1} = \frac{\sigma_\alpha^2 \sigma_K^2}{\sigma_\alpha^2 - \sigma_K^2}$$

and $\sigma > 0$ is equivalent to $\sigma_\alpha^2 > \sigma_K^2$ (cf. with conditions (i) and (ii) of Theorem 1 in Section 2).

Lemma A1. *Assume $\sigma > 0$. If $\sigma_2^2 \le 2\sigma^{-1}$, or if $\sigma_2^2 > 2\sigma^{-1}$ and*

$$\text{(A9)}\qquad u_1^2 \le \frac{2}{\sigma_\alpha^2} \ln\left[(e^r - 1)\left(\frac{\sigma_2^2\sigma}{2} - 1\right)\right] \sigma_K^2(\sigma_\alpha^2 - \sigma_K^2),$$

then equation (A2) does not have nontrivial period-two solutions. On the other hand, if $\sigma_2^2 > 2\sigma^{-1}$ *and*

$$u_1^2 > \frac{2}{\sigma_\alpha^2} \ln\left[(e^r - 1)\left(\frac{\sigma_2^2\sigma}{2} - 1\right)\right] \sigma_K^2(\sigma_\alpha^2 - \sigma_K^2), \tag{A10}$$

then equation (A2) has a unique nontrivial period-two solution and, consequently, (7) has a unique nontrivial period-two solution in $\{(x_1, x_2, u_2) \mid x_2 = 0\}$ *whose stable manifold is also contained in this set.*

Proof. Suppose (A2) has a period-two solution. Then there exists $\hat{u} \in \mathbb{R}$ such that $g(g(\hat{u})) = \hat{u}$. Straightforward calculation shows that $\beta'(2\bar{u} - u) = -\beta'(u)$, and $\beta(2\bar{u} - u) = \beta(u)$. Then, using (A3) and (A4), we rewrite $g(g(\hat{u})) = \hat{u}$ equivalently as

$$\frac{\beta'(g(\hat{u}))}{c_m e^{-\beta(g(\hat{u}))} + K_1} = -\frac{\beta'(\hat{u})}{c_m e^{-\beta(\hat{u})} + K_1},$$

or

$$\frac{\beta'(g(\hat{u}))}{c_m e^{-\beta(g(\hat{u}))} + K_1} = \frac{\beta'(2\bar{u} - \hat{u})}{c_m e^{-\beta(2\bar{u}-\hat{u})} + K_1}.$$

The function $\beta'(u)/(c_m e^{-\beta(u)} + K_1)$ is increasing in u. Hence, this equation is equivalent to $g(\hat{u}) = 2\bar{u} - \hat{u}$, that is,

$$e^{-\beta(\hat{u})}(\hat{u} - \bar{u}) = \frac{K_1}{c_m}\left(\frac{\sigma_2^2\sigma}{2} - 1\right)(\hat{u} - \bar{u}). \tag{A11}$$

In order for this equation to have a solution $\hat{u} \neq \bar{u}$, it must be true that $\sigma_2^2 > 2\sigma^{-1}$. Thus, if $\sigma_2^2 \leq 2\sigma^{-1}$, then this equation does not have any solutions $\hat{u}$, which means that (A2) does not have nontrivial period-two solutions.

Now assume $\sigma_2^2 > 2\sigma^{-1}$. Then (A11) has a real solution $\hat{u} \neq \bar{u}$ if and only if

$$\beta(\hat{u}) = -\ln\frac{K_1}{c_m}\left(\frac{\sigma_2^2\sigma}{2} - 1\right). \tag{A12}$$

Since $\beta(u)$ attains its minimum at $u = \bar{u}$, (A12) has solutions different from $\bar{u}$ if and only if

$$\beta(\bar{u}) < -\ln\frac{K_1}{c_m}\left(\frac{\sigma_2^2\sigma}{2} - 1\right). \tag{A13}$$

Using (A3), one can show that this inequality is equivalent to the inequality (A10). Thus, if (A9) holds, then (A12) has no solutions, which means that (A2) has no nontrivial period-two solutions. On the other hand, if (A10) holds, then (A12) has exactly two solutions, which means that (A2) has exactly one nontrivial period-two solution. Denote this solution by $\{\bar{v}, \bar{w}\}$. Hence $\gamma := \{(K_1, 0, \bar{v}), (K_1, 0, \bar{w})\}$ is a nontrivial, period-two solution of (7). This implies

$$\frac{e^r}{1 + c(\bar{v}, u_1)K_1} \frac{e^r}{1 + c(\bar{w}, u_1)K_1} > 1. \tag{A14}$$

There exists a neighborhood V of γ such that $(x_1(t), x_2(t), u_2(t)) \in V$ and $x_2(t) > 0$ imply $x_2(t+1) > x_2(t)$. This shows that no solution $(x_1(t), x_2(t), u_2(t))$ with $x_2(0) > 0$ converges to γ, which concludes the proof.

APPENDIX B: PROOF OF THEOREM 1

Let $(x_1(t), x_2(t), u_2(t))$ denote a forward bounded solution of (7) with $x_1(0) \geq 0$ and $x_2(0) > 0$. Let ω denote its forward limit set, which is a compact. Our goal is to prove that ω contains no point of the form $(x_1, 0, u_2)$.

For purposes of contradiction, assume there is a point $(x_1, 0, u_2) \in \omega$. Consider the solution $(x_1(t), 0, u_2(t))$ of (7) with initial condition $(x_1, 0, u_2)$. Then $x_1(t)$ and $u_2(t)$ satisfy (A1a)-(A1b) and

$$\lim \inf_{t \to +\infty} x_1(t) = \begin{cases} 0 & \text{if } x_1 = 0 \\ K_1 & \text{if } x_1 > 0 \end{cases}.$$

Thus, either $(0, 0, u_2)$ or $(K_1, 0, u_2)$ lie in ω. We complete the proof in two steps by showing:

Step (1). ω contains no point of the form $(0, 0, u_2)$.
Step (2). ω contains no point of the form $(K_1, 0, u_2)$.

Step (1). We write the system formed by the two equations (7a) and (7b) in the form

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = A(t, x_1(t), x_2(t)) \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix}, \tag{B1}$$

where

$$A(t, x_1(t), x_2(t)) := \begin{pmatrix} G(u_1, u_1, u_2(t), x_1(t), x_2(t)) & 0 \\ 0 & G(v, u_1, u_2(t), x_1(t), x_2(t))|_{v=u_2(t)} \end{pmatrix}.$$

Note that $A(t,0,0)=e^r I$ where I denotes the 2×2 identity matrix. Since $u_2(t)$ is bounded, there exist $\xi>1$ and $\delta>0$ such that for all (x_1,x_2) satisfying $0<x_1+x_2<\delta$ we have $|A(t,x_1,x_2)\eta|>\xi$ where η is a nonnegative unit vector. Note that

$$0\le x_i(t+1)\le x_i(t)\frac{e^r}{1+c(0,0)x_i(t)},\quad i=1,2.$$

Thus, $x_i(t)\to[0,K_m]$, $i=1,2$ and there exists $\varepsilon\in(0,\delta)$ such that

$$\varepsilon<\min\{|A(t,x_1,x_2)(x_1,x_2)^T|\mid t\ge 0 \text{ and } \delta\le x_1+x_2\le 2K_m\}.$$

This proves that

$$\liminf_{t\to\infty}\ (x_1(t)+x_2(t))\ge\varepsilon$$

and hence $(0,0,u_2)\notin\omega$.

Step (2). Suppose, for purposes of contradiction, that there exists a u_2 such that

$$(K_1,0,u_2)\in\omega. \tag{B2}$$

A calculation shows that

$$\frac{e^r}{1+c(\bar u,u_1)K_1}>1. \tag{B3}$$

Then there exists a neighborhood V of $(K_1,0,\bar u)$ such that $(x_1(t),x_2(t),u_2(t))\in V$ and $x_2(t)>0$ implies $x_2(t+1)>x_2(t)$. This shows that no solution $(x_1(t),x_2(t),u_2(t))$ with $x_1(0)\ge 0$ and $x_2(0)>0$ can converge to $(K_1,0,\bar u)$. Then, by the Butler–McGehee theorem (see Smith and Thieme [2011]), we know that there exists a point

$$\mathbf{x}=(x_1,0,u_2)\in\omega,\quad (x_1,0,u_2)\ne(K_1,0,\bar u),\quad x_1>0 \text{ (by Step 1)}. \tag{B4}$$

(a) Suppose $x_1\ne K_1$ in (B4). Let $\varphi(t):=(\varphi_1(t),\varphi_2(t),\varphi_3(t))$ be a total trajectory through $(x_1,0,u_2)\in\omega$ which therefore lies in ω for $t\in\mathbb{Z}$. Then $\varphi_1(t)$ satisfies (A1a) for all $t\in\mathbb{Z}$. Since this equation is of Beverton–Holt type and $\varphi(t)$ is either increasing or decreasing in $t\in\mathbb{Z}$, we have that $\varphi_1(t)\to 0$ or $\varphi_1(t)\to\infty$ as $t\to-\infty$. Both cases lead to a contradiction. In particular, $\varphi_1(t)\to 0$, as

$t \to -\infty$ contradicts the fact that no point of the form $(0, 0, u_2)$ can be in ω and $\varphi_1(t) \to \infty$ as $t \to -\infty$ contradicts the fact that ω is compact.

(b) Now suppose $x_1 = K_1$, that is, that $\mathbf{x} = (K_1, 0, u_2)$. Then, for the solution $(x_1(t), x_2(t), u_2(t))$ of (7) with initial condition $\mathbf{x} = (K_1, 0, u_2)$, it follows that $x_1(t) = K_1$ for all $t \geq 0$ and $u_2(t)$ satisfies (A2).

Case 1. If $\sigma_2^2 < \sigma^{-1}$ then $\lim_{u\to-\infty} g(u) = -\infty$ and $\lim_{u\to\infty} g(u) = \infty$. In this case, either

(i) g is increasing on one of the two intervals $(-\infty, v)$ or (w, ∞),
(ii) or there exist $c < v < a < \bar{u}$ and $d > w > b > \bar{u}$ such that g is increasing on $(-\infty, c) \cup (a, b) \cup (d, \infty)$ and decreasing on $(c, a) \cup (b, d)$.

Consider the first alternative (i). In this case, $g(u)$ is increasing on $\mathbb{R}$. Let $\varphi(t) = (\varphi_1(t), \varphi_2(t), \varphi_3(t))$ be a total trajectory of (7) through $(K_1, 0, u_2)$ This trajectory exists and lies in ω (Theorem 1.40, p. 20, in Smith and Thieme [2011]). But since $g(u)$ is increasing on $\mathbb{R}$ it follows $|\phi_3(t)| \to \infty$ as $t \to -\infty$, which is a contradiction to the compactness of ω. This rules out alternative (i).

Consider alternative (ii). Let I denote the basin of attraction of $\bar{u}$ for (A2). Clearly $[a, b] \subseteq I$. We claim that $I = \mathbb{R}$.

First note that, if $g^{-1}(b) \cap (c, a) = \emptyset$, then $g(u) \leq b$ for all $u \in (-\infty, \bar{u})$ and so, from (A4), we obtain $I = \mathbb{R}$. An analogous argument that $I = \mathbb{R}$ holds if $g^{-1}(a) \cap (b, d) = \emptyset$. Finally, suppose that $g^{-1}(b) \cap (c, a) \neq \emptyset$ and $g^{-1}(a) \cap (b, d) \neq \emptyset$. Then there exists $\bar{u}_1 \in (c, a)$ such that $g(\bar{u}_1) = b$ and $\bar{v}_1 \in (b, d)$ such that $g(\bar{v}_1) = a$. Then $[\tilde{u}_1, \tilde{v}_1] \subseteq I$. By repeating the reasoning above with a and b replaced respectively by $\tilde{u}_1$ and $\tilde{v}_1$, we obtain a decreasing sequence $(\tilde{u}_n)_{n\geq 1} \subset (c, a)$ and an increasing sequence $(\tilde{v}_n)_{n\geq 1} \subset (b, d)$, such that $[\tilde{u}_n, \tilde{v}_n] \subset I$ and $g(\tilde{u}_{n+1}) = \tilde{v}_n$, $g(\tilde{v}_{n+1}) = \tilde{u}_n$ for all $n \geq 1$. Let $\hat{u}$ and $\hat{v}$ be the limits of $(\tilde{u}_n)_n$ and $(\tilde{v}_n)_n$, respectively. Then, since g is continuous, we have $g(\hat{u}) = \hat{v}$ and $g(\hat{v}) = \hat{u}$, which means that $\{\hat{u}, \hat{v}\}$ are the two points of a period-two solution of (A2), whose existence is in contradiction to Lemma A1. Thus, the claim that we made earlier holds.

Let Z be the closure of the orbit considered at the beginning of the proof (hence Z is positively invariant), $X = \{(x_1, x_2, u_2) \mid x_2 = 0\}$, and $M = Z \cap X$. From Step (1) and (a) above, M can only contain points of the form $(K_1, 0, u_2)$. Also, according to (B2), $M \neq \emptyset$. Hence all solutions starting in M converge to $(K_1, 0, \bar{u})$. Then, using (B3) and applying Corollary 1 in Salceanu and Smith [2009], we have that M is a uniformly weak repeller (see definition in Salceanu and Smith [2009]). In particular, we have that there exists $\varepsilon > 0$ such that

$$\limsup_{t\to\infty} x_2(t) > \varepsilon, \tag{B5}$$

for every solution $(x_1(t), x_2(t), u_2(t))$ of system (7) that is contained in Z and has $x_2(0) > 0$. Then, since Z is a compact set, by applying Theorem 5.2 in Smith and Thieme [2011], we see that (B5) holds with "lim sup" replaced by "lim inf." But this contradicts (B2).

Case 2: If $\sigma_2^2 > \sigma^{-1}$, then $\lim_{u\to-\infty} g(u) = \infty$ and $\lim_{u\to\infty} g(u) = -\infty$. Thus, we have two possibilities: (1^0) either g is decreasing on $\mathbb{R}$, or (2^0) there exist two numbers $a \in (v, \bar{u})$ and $b \in (\bar{u}, w)$ such that g is decreasing in $(-\infty, a) \cup (b, \infty)$ and increasing in (a, b). Then, when either

(i) $\sigma_2^2 \leq 2\sigma^{-1}$ or
(ii) $\sigma_2^2 > 2\sigma^{-1}e^r/(e^r - 1)$ (which is equivalent to $(e^r - 1)(\sigma_2^2\sigma/2 - 1) > 1$) and (A9) holds

we conclude from Lemma A1 and the fact that $u > \bar{u} \iff g(u) < u$ (see (A4)) that a total trajectory through $\mathbf{x}$ would become unbounded. This would contradict that ω is compact and invariant.

If $\sigma_2^2 > 2\sigma^{-1}e^r/(e^r - 1)$ and (A10) holds, then the stable manifold of the unique, non-trivial periodic solution γ of (7) is contained in the set $\{(x_1, x_2, u_2) \mid x_2 = 0\}$ and so again, by applying the Butler–McGehee theorem, ω contains a point $(K_1, 0, \hat{u}_2)$ on the stable manifold of γ with $\hat{u}_2 \notin \{\bar{v}, \bar{w}\}$. Let $\varphi(t) = (\varphi_1(t), \varphi_2(t), \varphi_3(t))$ be a total trajectory through $(K_1, 0, \hat{u}_2)$. First suppose g is decreasing on $\mathbb{R}$. If $\varphi_3(t) \to \pm\infty$ as $t \to -\infty$ we have a contradiction to the fact that ω is compact and invariant. Otherwise, let $l_1 = \lim_{t\to-\infty} \phi_3(t)$ and $l_2 = \lim_{t\to\infty} \phi_3(t)$. Then $\{l_1, l_2\}$ is a periodic solution of (A2), different from $\gamma = \{(K_1, 0, \bar{v}), (K_1, 0, \bar{w})\}$, again a contradiction to Lemma A1. Next, suppose g is decreasing in $(-\infty, a) \cup (b, \infty)$ and increasing in (a, b). Then $\bar{v} \in (-\infty, a)$, $\bar{w} \in (b, \infty)$ and solutions of (A2) with initial condition in $(\bar{v}, \bar{w})$ converges to $\bar{u}$.

Hence $\hat{u}_2 \notin [\bar{v}, \bar{w}]$. Then, as above, it follows that either a total trajectory through $(K_1, 0, \hat{u}_2)$ becomes unbounded or there is a nontrivial period-two solution of (A2) different from $\{\bar{u}, \bar{v}\}$, both resulting in contradictions.

Case 3: If $\sigma_2^2 = \sigma^{-1}$ we have a similar situation to Case 2, with the only difference being that now $\lim_{u\to\pm\infty} g(u) = -\sigma_2^2 u_1/\sigma_\alpha^2$.

Appendix C: Proof of Theorem 2

First, we establish the existence of a compact attracting (or absorbing) set. To this end note that, from the proof of Theorem 1, $x_i(t)$ is attracted to $[0, K_m]$, $i = 1, 2$. Thus, it is left to show that u_2 is also attracted to a compact interval. To this end, we first claim that

$$\left|\frac{u_2(t+1)}{u_2\,(t)}\right| < 1 \text{ if } |u_2(t)| \text{ is sufficiently large.}$$

Note that

$$\text{(C1)}\qquad \begin{aligned}&\frac{u_2(t+1)}{u_2(t)}\\ &\quad = 1-\sigma_2^2\frac{(\sigma+\frac{u_1}{\sigma_\alpha^2 u_2(t)})c(u_2(t),u_1)x_1(t)+\frac{1}{\sigma_K^2}c(u_2(t),u_2(t))x_2(t)}{1+c(u_2(t),u_1)x_1(t)+c(u_2(t),u_2(t))x_2(t)}.\end{aligned}$$

Define

$$a := \sigma+\frac{u_1}{\sigma_\alpha^2 u_2},\quad 0<b:=\frac{1}{\sigma_K^2},\quad 0\leq x:=c(u_2,u_1)x_1,\quad 0\leq y:=c(u_2,u_2)x_2,$$

and note that

$$a=\frac{1}{\sigma_K^2}-\frac{1}{\sigma_\alpha^2}(1-\frac{u_1}{u_2})>0 \text{ and } a<b \text{ if } |u_2|>u^*:=\frac{1}{\sigma\sigma_\alpha^2}|u_1|.$$

It is then straightforward to prove that $|u_2|>u^*$ implies

$$\frac{ax+by}{1+x+y}\leq b<\frac{2}{\sigma_2^2}$$

which, using (C1) implies the claim.

Since the function, given by the right-hand side of the equation for u_2 in (7) is continuous on the set

$$\{(x_1,x_2,u_2)\mid 0\leq x_1,x_2\leq K_m \text{ and} -u^*\leq u_2\leq u^*\},$$

it has a minimum m_1 and a maximum m_2 on this set. Let $\hat{M}:=\max\{|m_1|,|m_2|,u^*\}$. Then, clearly, $u_2(t_0)\in[-u^*,u^*]$ implies $u_2(t)\in[-\hat{M},\hat{M}]$ for all $t\geq t_0$. Otherwise, assume $u_2(t)\notin[-u^*,u^*]$ for any $t\geq 0$. Then, since $|u_2(t)|$ is decreasing, we have that $|u_2(t)|\to l\geq 0$ as $t\to\infty$. Suppose $l>u^*$ for such a solution of (7) starting at $y_0=(x_1^0,x_2^0,u_2^0)$. Then $\omega(y_0)\subseteq\{(x_1,x_2,u_2)\mid |u_2|=l\}$.

Consider now the solution $(\tilde{x}_1(t),\tilde{x}_2(t),\tilde{u}_2(t))$ of (7) starting at $\tilde{y}_0=(\tilde{x}_1^0,\tilde{x}_2^0,\tilde{u}_2^0)\in\omega(y_0)$. Then, $|\tilde{u}_2(1)|<\tilde{u}_2(0)=l$, which contradicts the fact that $\omega(y_0)$ is invariant. Thus, every solution of (7) is attracted to the compact set $B:=\{(x_1,x_2,u_2)\mid 0\leq x_1,x_2\leq K_m \text{ and } |u_2|\leq\hat{M}\}$.

Let $X_{01}:=\{(x_1,x_2,u_2)\in X\mid x_2=0\}$ and $M_1:=B\cap X_{01}$ (hence M_1 is compact). Then, from the discussion, all solutions starting in M_1 converge to $(K_1,0,\bar{u})$. The conclusion now is obtained now from Proposition 3.3 and Theorem 3.2 in Salceanu [2011].

APPENDIX D: PROOF OF THEOREM 3

To study persistence of x_1, we need to understand the boundary dynamics in this case. To this end, let $x_1(t) = 0$ for all $t \geq 0$. Then

$$u_2(t+1) = u_2(t) - \frac{\sigma_2^2}{\sigma_K^2} \frac{u_2(t)c(u_2(t), u_2(t))x_2(t)}{1 + c(u_2(t), u_2(t))x_2(t)}. \tag{D1}$$

Thus, since $\sigma_K^2 > \sigma_2^2/2$, it follows that $u_2(t+1)/u_2(t) \in (-1, 1)$ for all t, hence $u_2(t) \to 0$ as $t \to \infty$. From this we conclude

$$x_2(t) \to K_2 := \frac{e^r - 1}{c(0,0)} = K_m.$$

Let $(x_1(t), x_2(t), u_2(t))$ denote a bounded solution of (7) with $x_1(0) > 0$ and $x_2(0) \geq 0$ and suppose that $\liminf_{t\to\infty} x_1(t) = 0$. Then ω, the omega limit set of this solution, contains a point of the form $(0, x_2, u_2)$. That no point of the form $(0, 0, u_2)$ can be in ω can be proved the same as in the proof of Theorem 1. Hence, from the preceding paragraph, we have that $(0, K_2, 0) \in \omega$.

Using that $\sigma < 0$, straightforward calculation shows that

$$\frac{e^r}{1 + c(u_1, 0)K_2} > 1.$$

Then, as in the proof of Theorem 1, there exists a neighborhood V of $(0, K_2, 0)$ such that

$$(x_1(t), x_2(t), u_2(t)) \in V \text{ and } x_1(t) > 0$$

imply $x_1(t+1) > x_1(t)$. This shows that no solution $(x_1(t), x_2(t), u_2(t))$ with $x_1(0) > 0$ converges to $(0, K_2, 0)$. Then, from the Butler–McGehee theorem, we have that ω contains a point of the form $(0, x_2, u_2)$ with $x_2 > 0$ and $u_2 \neq 0$. Then the solution of (7) starting at $(0, x_2, u_2)$ would have $|u_2(t)| \to \infty$ as $t \to -\infty$, hence we would have a contradiction to ω being bounded.

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