INTRASPECIFIC INTERFERENCE AND
CONSUMER-RESOURCE DYNAMICS

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ABSTRACT. In this paper we first consider a two consumer-one resource model with one of the consumer species exhibits intraspecific feeding interference but there is no interspecific competition between the two consumer species. We assume that one consumer species exhibits Holling II functional response while the other consumer species exhibits Beddington-DeAngelis functional response. Using dynamical systems theory, it is shown that the two consumer species can coexist upon the single limiting resource in the sense of uniform persistence. Moreover, by constructing a Liapunov function it is shown that the system has a globally stable positive equilibrium. Second, we consider a model with an arbitrary number of consumers and one single limiting resource. By employing practical persistence techniques, it is shown that multiple consumer species can coexist upon a single resource as long as all consumers exhibit sufficiently strong conspecific interference, that is, each of them exhibits Beddington-DeAngelis functional response.

1. **Introduction.** The principle of competitive exclusion is one of the best known results in theoretical ecology. In its most basic form (which dates back to the work of Volterra [40] in the 1920's), it asserts that two or more consumer species cannot coexist indefinitely on a single limiting resource. Volterra's theoretical observations were supported by experiments on *Paramecium* cultures by Gause [20] in the early 1930's (see also Kareiva [28]) and, by the 1960's, had become part of the orthodoxy of theoretical ecology. Indeed, the principle had been extended to assert that n consumer species require at least n limiting resources if they are to coexist in the long term (MacArthur and Levins [32]). It was recognized at that time that this theoretical observation was somehow at odds with the reality of natural systems (see, for example, the famous paper "The paradox of the plankton" by Hutchinson [25]) but was thought to hold in laboratory settings until 1969 when Ayala [2] demonstrated experimentally that two species of *Drosophila* could coexist upon a single limiting resource.

Ayala's experiments led to large body of work, which continues to this day, on factors that serve to mediate the coexistence of multiple consumers upon a single resource (for an overview of some of these factors and a number of references, see Cantrell and Cosner [10]). One key factor was identified rather early on in

the discussion by Schoener [35] in 1976. Namely, intraspecific interference among consumers may lead to coexistence of multiple consumer species upon a single resource. The purpose of this paper is to employ the theory of dynamical systems, particularly persistence theory, which did not exist in 1976, to examine more closely the implications of feeding interference among conspecific consumers on consumer-resource dynamics.

In order to put our efforts in this paper into context, we need to revisit very briefly the modeling regime behind the principle of competitive exclusion and also one of the many modifications of such models that appeared following Ayala's experiments with *Drosophila*. To this end, recall that the mathematical models which underlie the principle of competitive exclusion are based upon the principle of mass action. So in such a model the increase in the growth rate of a consumer species (or the decrease in the growth rate of a resource species) that is attributed to resource consumption is taken proportional to the encounters between the species. In the case of two consumers sharing a single limiting resource, one may consider

$$
\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - auv - Auw, \\
\frac{dv}{dt} &= v(-d + eu), \\
\frac{dw}{dt} &= w(-D + Eu),
\end{aligned}
\tag{1.1}
$$

where v and w are the densities of the two consumer species and u is the density of the resource. Ecologists frequently assume that the dynamics of a resource species occur on a considerably shorter time scale than those of consumer species. In the case of (1.1), such an assumption allows one to conclude that effectively the density of the resource species can be "tracked" in terms of the densities of consumer species, thus reducing (1.1) to the two-species competition model

$$
\begin{aligned}
\frac{dv}{dt} &= v\left(eK - d - \frac{aeK}{r}v - \frac{AeK}{r}w\right), \\
\frac{dw}{dt} &= w\left(EK - D - \frac{aEK}{r}v - \frac{AEK}{r}w\right).
\end{aligned}
\tag{1.2}
$$

Generically, the isoclines for the system (1.2) are parallel lines. As a consequence, in all but some very exceptional cases, the model (1.2) predicts either that species v always out competes species w for the resource and thus eliminates species w over time or that species w always out competes species v for the resource and thus eliminates species v over time.

Among the many modifications of (1.1) that appeared in the aftermath of Ayala's experiments, the one most relevant to our present discussion is due to Armstrong and McGehee [1], who considered the model

$$
\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - auv - \frac{Auw}{1 + Bu}, \\
\frac{dv}{dt} &= v(-d + eu), \\
\frac{dw}{dt} &= w\left(-D + \frac{Eu}{1 + Bu}\right),
\end{aligned}
\tag{1.3}
$$

where again v and w are the densities of the consumers and u is the density of the resource. The model (1.3) differs from (1.1) in two ways. First of all, the contributions of the interaction between consumer species w and the resource species u to the growth rates of those species are no longer accounted for by the principle of mass action. The term uw has been replaced with Holling II functional and numerical response terms. Secondly and somewhat more subtly, one no longer assumes that the resource dynamics occur on a much shorter time scale that do consumer dynamics, so (1.3) does not reduce to a two component system as with (1.1) and (1.2). However, in both (1.1) and (1.3), consumption of a common limiting resource is the only interaction between species v and w that is represented. Armstrong and McGehee [1] found that *for appropriate parameter values and suitable initial population densities* $(u(0), v(0), w(0))$, (1.3) does predict coexistence of the two consumers via a locally attracting periodic orbit. Hsu, Hubbell and Waltman [21, 22] generalized this type of coexistence to the case when both consumer species exhibit Holling II functional response (see also Butler and Waltman [5], Cushing [14], Farkas [16], Muratori and Rinaldi [34], Smith [37], etc.); i.e., to a system of the form

$$
\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{auv}{1+bu} - \frac{Auw}{1+Bu}, \\
\frac{dv}{dt} &= v\left(-d + \frac{eu}{1+bu}\right), \\
\frac{dw}{dt} &= w\left(-D + \frac{Eu}{1+Bu}\right).
\end{aligned}
\tag{1.4}
$$

Recently, Hsu, Hwang and Kuang [23] also studied the case when the two consumer species exhibit ratio-dependent functional responses. However, in most cases, such systems do not have a componentwise positive equilibrium.

The mathematical analysis employed by Armstrong and McGehee [33, 1] to support their conclusions is very much in the spirit of persistence theory, although their work predates much of the development of persistence theory. The principal notion of persistence theory is uniform persistence or permanence. Consider an ODE model for n interacting biological species

$$
\frac{du_i}{dt} = u_i f_i(u_1, u_2, \ldots, u_n), \quad i = 1, 2, \ldots, n,
\tag{1.5}
$$

where $u_i(t)$ denotes the density of the ith species. Let $(u_1(t), u_2(t), \ldots, u_n(t))$ denote the solution of (1.5) with componentwise positive initial values. The system (1.5) is said to be *weakly persistent* if

$$
\limsup_{t \to \infty} u_i(t) > 0, \quad i = 1, 2, \ldots, n,
\tag{1.6}
$$

persistent if

$$
\liminf_{t \to \infty} u_i(t) > 0, \quad i = 1, 2, \ldots, n
\tag{1.7}
$$

and *uniformly persistent* if there is an $\varepsilon_0 > 0$ such that

$$
\liminf_{t \to \infty} u_i(t) \geq \varepsilon_0, \quad i = 1, 2, \ldots, n.
\tag{1.8}
$$

The system (1.5) is said to be *permanent* if for each $i = 1, 2, \ldots, n$ there are constants ε_i and M_i such that

$$
0 < \varepsilon_i \leq \liminf_{t \to \infty} u_i(t) \leq \limsup_{t \to \infty} u_i(t) \leq M_i.
\tag{1.9}
$$

Clearly, a permanent system is uniformly persistent which in turn is persistent, and persistence implies weak persistence; a dissipative uniformly persistent system is permanent. For further discussion about various definitions of persistence and permanence and their connections, we refer to Freedman and Moson [17], Hutson and Schmitt [24], and Thieme [39].

Generally speaking, the term persistence is given to systems in which strictly positive solutions do not approach the boundary of the nonnegative cone in R^n. Weak persistence applies when it is required that positive solutions do not asymptotically approach the boundary as $t \to \infty$. Persistence means that each strictly positive solution is eventually at some distance from the boundary. Uniform persistence means that each strictly positive solution is eventually uniformly bounded away from the boundary, while permanence implies the existence of a closed, bounded set, say $\mathcal{A}$, of componentwise positive n-tuples (representing potential configurations of species densities) so that $\mathcal{A}$ is bounded away from the collection of n-tuples with at least one vanishing component (representing potential configurations of species densities with at least one species absent) and such that any trajectory of the model with componentwise positive initial densities converges to $\mathcal{A}$ as time tends to ∞. When long term coexistence of the consumer species does occur in (1.3) or (1.4), it usually depends on having suitable initial population densities. In some exceptional cases, weak persistence is possible in (1.3) and (1.4) but they cannot be persistent. The weaker form of coexistence has also been called *conditional persistence* in Cantrell and Cosner [9, 10]. (As an aside, it is also well-known (see Butler, Freedman and Waltman [4] and Hutson and Schmitt [24], for example) that permanent ODE models for interacting biological species exhibit componentwise positive equilibria. Consequently, the fact that (1.3) and (1.4) do not exhibit such equilibria is another "tip-off" that they cannot be permanent.)

In [10], Cantrell and Cosner extended (1.4) further so as to incorporate conspecific feeding interference for each consumer species. The resulting model is

$$
\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{auv}{1 + bu + cv} - \frac{Auw}{1 + Bu + Cw}, \\
\frac{dv}{dt} &= v\left(-d + \frac{eu}{1 + bu + cv}\right), \\
\frac{dw}{dt} &= w\left(-D + \frac{Eu}{1 + Bu + Cw}\right).
\end{aligned}
\tag{1.10}
$$

Notice that as with (1.1), (1.3) and (1.4), the only interaction in (1.10) between consumer species v and w is consumption of a common limiting resource. The functional and numerical responses for both consumers and the resource are now taken to have Beddington-DeAngelis [3, 15] form

$$
\frac{uv}{1 + bu + cv}, \quad \frac{uw}{1 + Bu + Cw}.
\tag{1.11}
$$

In (1.11), cv and Cw may be viewed as accounting for mutual feeding interference among members of consumer species. Note that if $c = C = 0$, a Beddington-DeAngelis form reduces to a Holling II form. For further discussion about the Beddington-DeAngelis functional response, we refer to Cosner et al. [13] and Skalski and Gilliam [36]. In [10], Cantrell and Cosner show that if conspecific interference is strong enough in (1.10) (i.e. c and C are sufficiently large), one may obtain

quantitatively explicit positive asymptotic upper and lower bounds on the components of solution trajectories, where the bounds are independent of initial densities so long as all initial densities are positive. Such results are referred to as *practical persistence* results, and they imply the permanence of (1.10) when c and C are large enough. Consequently, two consumer species may coexist in a very strong way upon single limiting resource so long as each exhibits strong enough self-interference in feeding.

In this article, we expand upon the preceding observation from [10] in two significant ways. First, in Section 2, we demonstrate that two consumers can in fact coexist upon a single limiting resource in the sense of uniform persistence when only one of the consumer species exhibits intraspecific feeding interference. To this end, we consider a modification of (1.10) wherein the functional and numerical response are relaxed to be of Holling II form, while those associated with the other species remain of Beddington-DeAngelis form. Our analysis sheds additional light upon the stabilizing effect of the mechanism of intraspecific feeding interference. In particular, we are able to show that permanence in the model corresponds to a globally attracting componentwise positive equilibrium.

The second way in which we expand upon the permanence results for (1.10) in [10] is to show that in fact an arbitrary number of consumers can coexist upon a single limiting resource provided all of them exhibit sufficiently strong conspecific feeding interference. In Section 3, we consider an extension of (1.10) to an arbitrary number of consumer species, in which the functional and numerical response terms associated with each consumer have Beddington-DeAngelis form, and employ practical persistence techniques to obtain a prediction of permanence in the model.

2. **One Resource and Two Consumers.** Let $u(t)$ represent the density of the limiting resource at time t. Assume that there are two consumer species, denoted by $v(t)$ and $w(t)$ respectively, competing for the common resource. We further assume that the first consumer feeds upon the resource according to the Holling II functional response while the second consumer feeds on the resource following the Beddington-DeAngelis functional response. The model is a system of three differential equations of the form

$$\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{auv}{1 + bu} - \frac{Auw}{1 + Bu + Cw}, \\
\frac{dv}{dt} &= v\left(-d + \frac{eu}{1 + bu}\right), \\
\frac{dw}{dt} &= w\left(-D + \frac{Eu}{1 + Bu + Cw}\right)
\end{aligned} \tag{2.1}$$

under the initial value conditions

$$u(0) = u_0 \geq 0, \quad v(0) = v_0 \geq 0, \quad w(0) = w_0 \geq 0. \tag{2.2}$$

2.1. **Dissipativity.** First of all, we can see that the solutions to the initial value problem (2.1) - (2.2) are nonnegative. We also have the following results on the boundedness of solutions of system (2.1).

PROPOSITION 2.1. *System (2.1) is dissipative.*

Proof. From the first equation in system (2.1) we have

$$\frac{du}{dt} \le ru\left(1 - \frac{u}{K}\right),$$

so that the comparison principle implies that

$$\limsup_{t \to \infty} u(t) \le K.$$

Thus, for $\varepsilon > 0$ small, we have $u(t) \le K + \varepsilon$ when t is sufficiently large. Denote $d_0 = \min\{d, D\}$. From the three equations in (2.1) we have

$$
\begin{aligned}
\frac{du}{dt} + \frac{a}{e}\frac{dv}{dt} + \frac{A}{E}\frac{dw}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{ad}{e}v - \frac{AD}{E}w \\
&\le ru - d_0\left(\frac{a}{e}v + \frac{A}{E}w\right),
\end{aligned}
$$

which implies that

$$\frac{d}{dt}\left(u + \frac{a}{e}v + \frac{A}{E}w\right) \le (r + d_0)(K + \varepsilon) - d_0\left(u + \frac{a}{e}v + \frac{A}{E}w\right).$$

Using the comparison principle a second time, we have

$$\limsup_{t \to \infty}\left(u + \frac{a}{e}v + \frac{A}{E}w\right) \le \frac{(r + d_0)(K + \varepsilon)}{d_0},$$

which implies that system (2.1) is dissipative.

2.2. Subsystems.

Each consumer can survive by feeding on the resource in the absence of the other consumer. Correspondingly, there are two two-species subsystems to be considered. In the following, we review some known results on the dynamics of the two subsystems, both of which are predator-prey systems.

2.2.1. *Subsystem I – Holling II.* We first consider the predator-prey system with Holling II functional response:

$$
\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{auv}{1 + bu}, \\
\frac{dv}{dt} &= v\left(-d + \frac{eu}{1 + bu}\right).
\end{aligned}
\tag{2.3}
$$

The subsystem (2.3) has an interior equilibrium $\bar{E} = (\bar{u}, \bar{v})$ if

$$d < \frac{e}{b}, \tag{2.4}$$

where

$$\bar{u} = \frac{d}{e - bd}, \quad \bar{v} = \frac{re}{ad}\bar{u}\left(1 - \frac{\bar{u}}{K}\right). \tag{2.5}$$

The subsystem (2.3) has been studied by many researchers (e.g. Kuang and Freedman [29], Liou and Cheng [30], and various references cited therein) and its dynamics are very well understood. Here we summarize these results as follows:

PROPOSITION 2.2. *Assume condition (2.4) holds.*

(i) *If $\frac{d}{e-bd} < K < \frac{e+bd}{b(e-bd)}$, then $\bar{E}$ is locally stable (and also globally stable).*

(ii) *If $K > \frac{e+bd}{b(e-bd)}$, then $\bar{E}$ is unstable and there is a unique stable limit cycle surrounding $\bar{E}$.*

2.2.2. *Subsystem II – Beddington-DeAngelis.* Now we consider the predator-prey system with Beddington-DeAngelis functional response:

$$\begin{aligned}
\frac{du}{dt} &= ru\left(1 - \frac{u}{K}\right) - \frac{Auw}{1 + Bu + Cw}, \\
\frac{dw}{dt} &= w\left(-D + \frac{Eu}{1 + Bu + Cw}\right).
\end{aligned} \tag{2.6}$$

There is an interior equilibrium $\tilde{E} = (\tilde{u}, \tilde{v})$ if

$$D < \frac{E}{B}, \tag{2.7}$$

where

$$\begin{aligned}
\tilde{u} &= \frac{rKCE - AK(E - BD) + \sqrt{[AK(E - BD) - rKCE]^2 + 4rACDE}}{2rCE}, \\
\bar{w} &= \frac{rE}{AD}\tilde{u}(1 - \frac{\tilde{u}}{D}).
\end{aligned} \tag{2.8}$$

The Jacobian matrix of system (2.6) at $\tilde{E}$ is given by

$$\tilde{J} = \left[\begin{array}{cc}
-\frac{r\tilde{u}}{K} + \frac{ABD\tilde{w}}{E(1+B\tilde{u}+C\tilde{w})} & -\frac{AD(1+B\tilde{u})}{E(1+B\tilde{u}+C\tilde{w})} \\
\frac{E\tilde{w}(1+C\tilde{w})}{(1+B\tilde{u}+C\tilde{w})^2} & \frac{CD\tilde{w}}{1+B\tilde{u}+C\tilde{w}}
\end{array}\right].$$

We can verify that $\det\tilde{J} > 0$. So the stability of $\tilde{E}$ is determined by $\mathrm{tr}\tilde{J}$. The stability of $\tilde{E}$ and the existence of limit cycles in the subsystem (2.6) were studied in Cantrell and Cosner [8]. The global stability of $\tilde{E}$ and the uniqueness of a limit cycle were recently investigated by Hwang [26, 27]. Their results can be summarized as follows:

PROPOSITION 2.3. *Assume condition (2.4) holds. Denote*

$$\mathrm{tr}\tilde{J} = \frac{r\tilde{u}}{K} + \frac{(CE - AB)D\tilde{w}}{E(1 + B\tilde{u} + C\tilde{w})}.$$

(i) *If* $\mathrm{tr}\tilde{J} < 0$, *then* $\tilde{E}$ *is not only locally stable but also globally stable.*
(ii) *If* $\mathrm{tr}\tilde{J} > 0$, *then* $\tilde{E}$ *is unstable and there exists a unique stable limit cycle surrounding* $\tilde{E}$.

2.3. **Uniform Persistence.** In this subsection we are concerned about persistence of the general system (2.1). We need to know the dynamics on the boundaries in the positive octant.

Let $f(u, v, w), g(u, v)$, and $h(u, w)$ represent the functions on the right-hand side of system (2.1), respectively. Then the Jacobian matrix of system (2.1) takes the form

$$J(u, v, w) = \left[\begin{array}{ccc}
f_u & f_v & f_w \\
g_u & g_v & 0 \\
h_u & 0 & h_w
\end{array}\right], \tag{2.9}$$

where

$$f_u = r\left(1 - \frac{u}{K}\right) - \frac{av}{1+bu} - \frac{Aw}{1+Bu+Cw} + u\left[-\frac{r}{K} + \frac{abv}{(1+bu)^2} + \frac{ABw}{(1+Bu+Cw)^2}\right],$$

$$f_v = -\frac{au}{1+bu}, \qquad f_w = -\frac{Au(1+Bu)}{(1+Bu+Cw)^2},$$

$$g_u = \frac{ev}{(1+bu)^2}, \qquad g_v = -d + \frac{eu}{1+bu},$$

$$h_u = \frac{Ew(1+Cw)}{(1+Bu+Cw)^2}, \qquad h_w = -D + \frac{Eu}{1+Bu+Cw} - \frac{CEuw}{(1+Bu+Cw)^2}.$$

We now consider the equilibria and periodic solutions on the boundaries.

(a) $E_0 = (0,0,0)$. The trivial equilibrium E_0 always exists and is a saddle, where the (v,w)-plane is the stable subspace and the u-axis is the unstable subspace.

(b) $E_K = (K,0,0)$. The semi-trivial equilibrium E_K is also a saddle if

$$(i)\ d < \frac{eK}{1+bK} \quad \text{and} \quad (ii)\ D < \frac{EK}{1+BK}. \qquad (2.10)$$

The u-axis is the stable subspace while the (v,w)-plane is the unstable subspace.

(c) $E_{uv} = (\bar{u}, \bar{v}, 0)$. E_{uv} is a boundary equilibrium on the (u,v)-plane, where $\bar{u}$ and $\bar{v}$ are given by (2.5). The Jacobian matrix is given by

$$J_{uv} = \begin{bmatrix} \bar{u}\left(-\frac{r}{K} + \frac{ab\bar{v}}{(1+b\bar{u})^2}\right) & -\frac{a\bar{u}}{1+b\bar{u}} & -\frac{A\bar{u}}{1+B\bar{u}} \\ \frac{e\bar{v}}{(1+b\bar{u})^2} & 0 & 0 \\ 0 & 0 & -D + \frac{E\bar{u}}{1+B\bar{u}} \end{bmatrix}$$

and the characteristic equation is

$$\left[\lambda^2 - \bar{u}\left(-\frac{r}{K} + \frac{ab\bar{v}}{(1+b\bar{u})^2}\right)\lambda + \frac{ad\bar{v}}{(1+b\bar{u})^2}\right]\left(\lambda + D - \frac{E\bar{u}}{1+B\bar{u}}\right) = 0.$$

If the conditions in Proposition 2.2(i) are satisfied, then the equilibrium $\bar{E}$ on the (u,v)-plane is stable, that is, E_{uv} is stable restricted to the (u,v)-plane. The eigenvalue in the w-axis direction is given by

$$\lambda_w = -D + \frac{E\bar{u}}{1+B\bar{u}}.$$

Thus, if

$$D > \frac{E\bar{u}}{1+B\bar{u}}, \qquad (2.11)$$

then E_{uv} is locally stable and if

$$D < \frac{E\bar{u}}{1+B\bar{u}}, \qquad (2.12)$$

then it is a saddle, where the w-axis is the unstable subspace.

(d) $E_\phi = (\phi_u, \phi_v, 0)$. If the conditions in Proposition 2.2 (ii) are satisfied, then the equilibrium $\bar{E}$ on the (u,v)-plane is unstable and there is a unique stable limit cycle on the (u,v)-plane, denoted by $(\phi_u(t), \phi_v(t))$. Consequently, $E_\phi = (\phi_u(t), \phi_v(t), 0)$ is a boundary periodic solution for the general system (2.1). Since E_ϕ is stable restricted to the (u,v)-plane, we only need to discuss its stability in the w-axis direction.

The stability of E_ϕ is determined by the Floquet multipliers of the variational system

$$\dot{\Phi}(t) = J(\phi_u, \phi_v, 0)\Phi(t), \quad \Phi(0) = I, \tag{2.13}$$

where $J(u, v, w)$ is defined in (2.9) and I is the 3×3 identity matrix. Let ω be the period of the periodic solution. Then the Floquet multiplier corresponding to the w direction is given by

$$\exp\left[\frac{1}{\omega}\int_0^\omega \left(-D + \frac{E\phi_u(t)}{1 + B\phi_u(t)}\right)dt\right].$$

Thus, if

$$D > \int_0^\omega \frac{E\phi_u(t)}{1 + B\phi_u(t)}dt, \tag{2.14}$$

then E_ϕ is stable and if

$$D < \int_0^\omega \frac{E\phi_u(t)}{1 + B\phi_u(t)}dt, \tag{2.15}$$

then it is unstable in the w-axis direction.

(e) $E_{uw} = (\tilde{u}, 0, \tilde{w})$. Similarly, E_{uw} is a boundary equilibrium on the (u, w)-plane, where $\tilde{u}$ and $\tilde{w}$ are given in (2.8). As was the case in (c), we know that if the conditions in Proposition 2.3(i) are satisfied, then the equilibrium $\tilde{E}$ on the (u, w)-plane is stable, that is, E_{uw} is stable restricted to the (u, w)-plane. The eigenvalue in the v-axis direction is given by

$$\lambda_v = -d + \frac{e\tilde{u}}{1 + b\tilde{u}}.$$

Thus, if

$$d > \frac{e\tilde{u}}{1 + b\tilde{u}}, \tag{2.16}$$

then E_{uw} is locally stable and if

$$d < \frac{e\tilde{u}}{1 + b\tilde{u}}, \tag{2.17}$$

then it is a saddle, with the v-axis as the unstable subspace.

(f) $E_\psi = (\psi_u(t), 0, \psi_w(t))$. If the conditions in Proposition 2.3(ii) are satisfied, then there is a unique limit cycle on the (u, w)-place, denoted by $(\psi_u(t), \psi_w(t))$. Then $E_\psi = (\psi_u(t), 0, \psi_w(t))$ is a boundary periodic solution for the general system (2.1). As in (d), we obtain that if

$$d > \int_0^\omega \frac{e\psi_u(t)}{1 + b\psi_u(t)}dt, \tag{2.18}$$

then E_ψ is stable and if

$$d < \int_0^\omega \frac{e\psi_u(t)}{1 + b\psi_u(t)}dt, \tag{2.19}$$

then it is unstable in the v-axis direction.

REMARK 2.4. Notice that d is required to be less than $\frac{e}{b}$, $\frac{eK}{1+bK}$, and $\frac{e\tilde{u}}{1+b\tilde{u}}$ in (2.4), (2.10)(i), and (2.17), respectively. Since $\frac{eu}{1+bu}$ is an increasing function in $u > 0$ and $\tilde{u} < K$, we have

$$\frac{e\tilde{u}}{1 + b\tilde{u}} < \frac{eK}{1 + bK} < \frac{e}{b}.$$

Thus, if (2.17) holds, then (2.4) and (2.10)(i) hold. Similarly, (2.12) holds, then (2.7) and (2.10)(ii) hold.

To obtain uniform persistence of the whole system (2.1), we employ the Acyclicity Theorem of Butler, Freedman and Waltman [4, 6]. To this end, we must ensure that the boundary equilibria and periodic orbits do not form a heteroclinic cycle, which is the acyclicity condition in the uniform persistence theorem in Butler, Freedman and Waltman [4] and Butler and Waltman [6] (see also Freedman, Ruan and Tang [19] and Yang and Ruan [41]).

Recall that both E_0 and E_K are saddles. E_{uv} is unstable in the w-axis direction if (2.12) holds, E_ϕ is unstable in the w-axis direction if (2.15) holds, E_{uw} is unstable in the v-axis direction if (2.17) holds, and E_ψ is unstable in the w-axis direction if (2.19) holds.

We now have the main theorem in this section.

THEOREM 2.5. *If the boundary equilibria E_{uv} and E_{uw} exist, assume (2.12) and (2.17) hold; if the boundary periodic orbits E_ϕ and E_ψ exist, assume (2.15) and (2.19) hold. Then system (2.1) is uniformly persistent.*

REMARK 2.6. In the case of boundary equilibria, the uniform persistence conditions are (2.12) and (2.17).

(a) Since $d = \frac{e\bar{u}}{1+b\bar{u}}$, condition (2.17) means that

$$\frac{e\bar{u}}{1+b\bar{u}} < \frac{e\tilde{u}}{1+b\tilde{u}}. \qquad (2.20)$$

Since $\frac{eu}{1+bu}$ is increasing, the above inequality requires that $\bar{u} < \tilde{u}$. Thus, to have long term survival of both consumers on the common resource, $\bar{u}$, the u-component of E_{uv} (the boundary equilibrium without interference) must be less than $\tilde{u}$, the u-component of E_{uw} (the boundary equilibrium with interference).

(b) It is well-known that the system is not uniformly persistent if $C = 0$, that is, if w also satisfies the Holling II functional response (Hsu, Hubbell and Waltman [21, 22]). Let us see how the introduction of C (the interference constant) can make the system uniformly persistent. Since $\bar{u} < \tilde{u}$, we have

$$\frac{E\bar{u}}{1+B\bar{u}} < \frac{E\tilde{u}}{1+B\tilde{u}}. \qquad (2.21)$$

Also, since $D = \frac{E\tilde{u}}{1+B\tilde{u}+C\tilde{w}}$, condition (2.12) is equivalent to

$$\frac{E\tilde{u}}{1+B\tilde{u}+C\tilde{w}} < \frac{E\bar{u}}{1+B\bar{u}}. \qquad (2.22)$$

Thus, assuming the inequality (2.21) holds, if we introduce the interference constant C with

$$C \geq \frac{\tilde{u}-\bar{u}}{\bar{u}\tilde{w}},$$

then the inequality (2.22) holds and the system (2.1) is uniformly persistent, and in fact, permanent.

(c) Notice that the proof of dissipativity does not depend upon C. So the quantity $(\tilde{u}-\bar{u})/\bar{u}\tilde{w}$ should be bounded above independent of the size of C even though $\bar{u}$ and $\tilde{w}$ depend on C. So we can obtain (2.22).

2.4. **Local and Global Stability of the Interior Equilibrium.** The dissipativity and uniform persistence of the system now guarantee (see Butler, Freedman and Waltman [4] and Hutson and Schmitt [24])) that system (2.1) has an interior

equilibrium $E^* = (u^*, v^*, w^*)$, where

$$u^* = \frac{d}{e - bd},$$

$$v^* = \frac{e}{ad}\left\{ru^*(1 - \frac{u^*}{K}) - \frac{A}{CE}\left[(E - BD)u^* - D\right]\right\}, \qquad (2.23)$$

$$w^* = \frac{(E - BD)u^* - D}{CD}.$$

REMARK 2.7.   Notice that u^*, the u-component of the interior equilibrium E^*, is equal to $\bar{u}$, the u-component of the boundary equilibrium E_{uv} without interference.

The Jacobian matrix of system (2.1) at E^* takes the form

$$J^* = \begin{bmatrix} f_u^* & f_v^* & f_w^* \\ g_u^* & 0 & 0 \\ h_u^* & 0 & h_w^* \end{bmatrix}, \qquad (2.24)$$

where

$$f_u^* = u^*\left[-\frac{ru^*}{K} + \frac{abv^*}{(1 + bu^*)^2} + \frac{ABw^*}{(1 + Bu^* + Cw^*)^2}\right], \qquad f_v^* = -\frac{au^*}{1 + bu^*} < 0,$$

$$f_w^* = -\frac{Au^*(1 + Bu^*)}{(1 + Bu^* + Cw^*)^2} < 0, \qquad g_u^* = \frac{ev^*}{(1 + bu^*)^2} > 0,$$

$$h_u^* = \frac{Ew^*(1 + Cw^*)}{(1 + Bu^* + Cw^*)^2} > 0, \qquad h_w^* = -\frac{CEu^*w^*}{(1 + Bu^* + Cw^*)^2} < 0.$$

The characteristic equation is given by

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \qquad (2.25)$$

where

$$a_1 = -(f_u^* + h_w^*), \quad a_2 = f_u^*h_w^* - f_w^*h_u^* - f_v^*g_u^*, \quad a_3 = f_v^*g_u^*h_w^*.$$

Since $a_3 > 0$, by Routh-Hurwitz criteria we have the following result on the local stability of E^*.

THEOREM 2.8.   *Assume that*

$$a_1 = -(f_u^* + h_w^*) > 0 \qquad (2.26)$$

and

$$a_1a_2 - a_3 = -f_u^*(f_u^*h_w^* - f_w^*h_u^* - f_v^*g_u^*) - h_w^*(f_u^*h_w^* - f_w^*h_u^*) > 0, \qquad (2.27)$$

then the interior equilibrium E^* is locally stable.

Finally, we give a sufficient condition for the global stability of the interior equilibrium E^*.

THEOREM 2.9.   *If*

$$\max\{b, B\}(K - u^*) < 1, \qquad (2.28)$$

then the interior equilibrium E^* is globally stable.

Proof.   Choose a Liapunov function as follows:

$$V(u, v, w) = \alpha \int_{u^*}^{u} \frac{x - u^*}{x}dx + \beta \int_{v^*}^{v} \frac{y - v^*}{y}dy + \gamma \int_{w^*}^{w} \frac{z - w^*}{z}dz, \qquad (2.29)$$

where α, β, and γ are positive constants to be determined. Along any trajectory of system (2.1), we have

$$
\begin{aligned}
\frac{dV}{dt} &= \alpha(u - u^*)\Big[r(1 - \frac{u}{K}) - \frac{av}{1 + bu} - \frac{Aw}{1 + Bu + Cw}\Big] \\
&\quad + \beta(v - v^*)\Big(-d + \frac{eu}{1 + bu}\Big) + \gamma(w - w^*)\Big(-D + \frac{Eu}{1 + Bu + Cw}\Big) \\
&= \alpha(u - u^*)\Big[-\frac{r(u - u^*)}{K} - \Big(\frac{av}{1 + bu} - \frac{av^*}{1 + bu^*}\Big) \\
&\qquad\qquad\qquad - \Big(\frac{Aw}{1 + Bu + Cw} - \frac{Aw^*}{1 + Bu^* + Cw^*}\Big)\Big] \\
&\quad + \beta(v - v^*)\Big(\frac{eu}{1 + bu} - \frac{eu^*}{1 + bu^*}\Big) \\
&\quad + \gamma(w - w^*)\Big(\frac{Eu}{1 + Bu + Cw} - \frac{Eu^*}{1 + Bu^* + Cw^*}\Big) \\
&= \alpha\Big[-\frac{r}{K} + \frac{abv^*}{(1 + bu)(1 + bu^*)} + \frac{ABw^*}{(1 + Bu + Cw)(1 + Bu^* + Cw^*)}\Big](u - u^*)^2 \\
&\quad + \frac{1}{1 + bu}\Big[-\alpha a + \beta e - \frac{\beta beu^*}{1 + bu^*}\Big](u - u^*)(v - v^*) \\
&\quad + \Big[-\alpha A + \frac{\alpha ACw^*}{1 + Bu^* + Cw^*} + \gamma E - \frac{\gamma BEu^*}{1 + Bu^* + Cw^*}\Big]\frac{(u - u^*)(w - w^*)}{1 + Bu + Cw} \\
&\quad - \frac{\gamma CD}{1 + Bu + Cw}(w - w^*)^2.
\end{aligned}
$$

Choose

$$
\alpha = 1, \quad \beta = \frac{a}{e - bd}, \quad \gamma = \frac{A(Eu^* - CDw^*)}{Eu^*(E - BD)}.
$$

Since

$$
D = \frac{Eu^*}{1 + Bu^* + Cw^*} < \frac{Eu^*}{Cw^*},
$$

we can see that $\gamma > 0$. Therefore,

$$
\begin{aligned}
\frac{dV}{dt} &= \Big[-\frac{r}{K} + \frac{abv^*}{(1 + bu)(1 + bu^*)} + \frac{ABw^*}{(1 + Bu + Cw)(1 + Bu^* + Cw^*)}\Big](u - u^*)^2 \\
&\quad - \frac{ACD(Eu^* - CDw^*)}{Eu^*(E - BD)(1 + Bu + Cw)}(w - w^*)^2.
\end{aligned}
$$

The coefficient for $(w - w^*)^2$ is always negative. The coefficient for $(u - u^*)^2$ is

$$
\begin{aligned}
&-\frac{r}{K} + \frac{abv^*}{(1 + bu)(1 + bu^*)} + \frac{ABw^*}{(1 + Bu + Cw)(1 + Bu^* + Cw^*)} \\
&\quad \leq -\frac{r}{K} + \frac{abv^*}{1 + bu^*} + \frac{ABw^*}{1 + Bu^* + Cw^*} \\
&\quad \leq -\frac{r}{K} + \max\{b, B\}\Big(\frac{av^*}{1 + bu^*} + \frac{ABw^*}{1 + Bu^* + Cw^*}\Big) \\
&\quad \leq -\frac{r}{K}\Big[1 - \max\{b, B\}(K - u^*)\Big].
\end{aligned}
$$

Thus, if (2.28) is satisfied, then $\frac{dV}{dt} \leq 0$ and $\frac{dV}{dt} = 0$ if and only if $u = u^*, v = v^*, w = w^*$. The largest invariant subset of the set of the points where $\frac{dV}{dt} = 0$ is

(u^*, v^*, w^*). Therefore, LaSalle's Invariance Principle implies that $E^* = (u^*, v^*, w^*)$ is globally stable. This completes the proof.

3. **One Resource and Many Consumers.** In this section we will show that it is possible for an arbitrary number of consumers to persist on a single resource provided that all consumers have a Beddington-DeAngelis functional response with suitable parameter values. Note that the only mechanism for mutual interference by consumers is the intraspecific feeding interference embodied in the Beddington-DeAngelis functional response. Our analytic approach is based on the notion of practical persistence (Cantrell and Cosner [7] and Cosner [12]). The key idea is to obtain asymptotic upper and lower bounds on densities by comparing each equation for the density of a species in the model with equations for best case and worst case scenarios.

The system we shall consider is

$$\begin{aligned}
\frac{du}{dt} &= ru\Big(1 - \frac{u}{K}\Big) - \sum_{i=1}^{n} \frac{A_i u w_i}{1 + B_i u + C_i w_i}, \\
\frac{dw_i}{dt} &= w_i\Big(-D + \frac{E_i u}{1 + B_i u + C_i w_i}\Big), \quad i = 1, 2, \ldots, n,
\end{aligned} \tag{3.1}$$

where $u(t)$ represents the density of the resource and $w_i(t)(i = 1, 2, \ldots, n)$ denotes the density of the ith consumer species at time t, respectively. Let

$$\overline{A} = \max_{1 \leq i \leq n} \{A_i\}, \quad \underline{A} = \min_{1 \leq i \leq n} \{A_i\},$$

and define $\overline{B}, \underline{B}, \overline{C}, \underline{C}$, etc. analogously. The positive orthant is invariant under (3.1), and we will consider only positive solutions. As in the proof of Proposition 2.1, we can show that

$$\frac{d}{dt}\Big(u + \sum_{i=1}^{n} \frac{A_i}{E_i} w_i\Big) \leq (r + \underline{D})(K + \varepsilon) - \underline{D}\Big(u + \sum_{i=1}^{n} \frac{A_i}{E_i} w_i\Big),$$

which implies that

$$\limsup_{t \to \infty} \Big(u + \sum_{i=1}^{n} \frac{A_i}{E_i} w_i\Big) \leq \frac{(r + \underline{D})(K + \varepsilon)}{\underline{D}}.$$

Thus, we have:

PROPOSITION 3.1. *The system (3.1) is dissipative.*

Let

$$\overline{w} = \frac{(\overline{E} - \underline{B}\,\underline{D})K - \underline{D}}{\underline{C}\,\underline{D}}.$$

To formulate and derive a persistence result we will use the following hypotheses:

$$(\underline{E} - \overline{B}\,\overline{D})K - \overline{D} > 0, \tag{3.2}$$

$$r - \frac{n\overline{A}\,\overline{w}}{1 + \underline{C}\overline{w}} = r - \frac{n\overline{A}[(\overline{E} - \underline{B}\,\underline{D})K - \underline{D}]}{\underline{C}(\overline{E} - \underline{B}\,\underline{D})K} > 0, \tag{3.3}$$

$$K(\underline{E} - \overline{B}\,\overline{D})\Big(1 - \frac{n\overline{A}\,\overline{w}}{r(1 + \underline{C}\overline{w})}\Big) - \overline{D} > 0. \tag{3.4}$$

Note that (3.3) and (3.4) imply (3.2) and that (3.2) implies

$$(\overline{E} - \underline{B}\,\underline{D})K - \underline{D} > 0, \tag{3.5}$$

which in turn implies $\overline{w} > 0$. Furthermore, note that $\underline{C}\,\overline{w}$ does not depend on $\underline{C}$, but $\overline{w} \to 0$ as $\underline{C} \to \infty$. It follows that (3.3)-(3.5) will be satisfied if (3.2) holds and $\underline{C}$ is sufficiently large.

THEOREM 3.2.   *Suppose that (3.3)-(3.5) hold. Then for any solution to (3.1) with all components initially positive and any $\varepsilon > 0$, there is a $T > 0$ such that for $t > T$,*

$$u \geq K\Big[1 - \frac{n\overline{A}\,\overline{w}}{r(1 + \underline{C}\overline{w})}\Big] - \varepsilon \tag{3.6}$$

and

$$w_i \geq \frac{K(\underline{E} - \overline{B}\,\overline{D})}{\overline{C}\,\overline{D}}\Big[1 - \frac{n\overline{A}\,\overline{w}}{r(1 + \underline{C}\overline{w})}\Big] - \overline{D} - \varepsilon, \;\; i = 1, 2, \ldots, n. \tag{3.7}$$

REMARK 3.3.   By the discussion following (3.5), the hypotheses (3.3) and (3.4) will hold and (3.6) and (3.7) will yield positive lower bounds on u and $w_i, i = 1, 2, \ldots, n$, provided $\overline{C} = \min_{1 \leq i \leq n}\{C_i\}$ is sufficiently large.

Proof.   The proof is based on two observations: First, if

$$\frac{du}{dt} \geq f(u) \;\text{ and }\; \frac{dw}{dt} \leq g(w)$$

with $f(s) \geq g(s)$ and $u(0) \geq w(0)$, then $u(t) \geq w(t)$ for all t. This is a standard comparison principle, which extends to reaction-diffusion equations among other types of models; see Cantrell and Cosner [7] and Cosner [12], for example. Second, if $f(u)$ is smooth and has the properties $f(0) = f(K) = 0$ and

$$f(u) \begin{cases} > 0 \;\text{ for }\;\; 0 < u < K, \\ < 0 \;\text{ for }\;\; u > K, \end{cases}$$

then any solution to $du/dt = f(u)$ which is initially positive must approach K as $t \to \infty$. In particular, for any $\varepsilon > 0$ there is a t_1 such that

$$K - \varepsilon \leq u(t) \leq K + \varepsilon \;\text{ for }\; t > t_1.$$

For the first inequality we will write $u \to\geq K$ to indicate that u is asymptotically greater than or equal to K. Symmetrically, we will write $u \to\leq K$ to indicate that u is asymptotically less than or equal to K.

Suppose $(u, w_1, \ldots, w_n)$ is a solution to (3.1) with all components initially positive, we have

$$\frac{du}{dt} \leq ru\Big(1 - \frac{u}{K}\Big),$$

so if $u(0) > 0$ then $u \to\leq K$ since all solutions to

$$\frac{du}{dt} = ru\Big(1 - \frac{u}{K}\Big)$$

which are positive at $t = 0$ approach K as $t \to \infty$. Thus, for any $\varepsilon_1 > 0$ there is a t_1 so that $u(t) \leq K + \varepsilon_1$ for $t > t_1$. For $t > t_1$ we also have

$$\begin{aligned}
\frac{dw_i}{dt} \;&\leq\; w_i\Big(\frac{E_i(K + \varepsilon_1)}{1 + B_i(K + \varepsilon_1) + C_i w_i} - D_i\Big) \\
&\leq\; w_i\Big(\frac{\overline{E}(K + \varepsilon_1)}{1 + \underline{B}(K + \varepsilon_1) + \underline{C}w_i} - \underline{D}\Big).
\end{aligned} \tag{3.8}$$

If ε_1 is sufficiently small and (3.5) holds then all positive solutions of

$$\frac{dw}{dt} = w\Big(\frac{\overline{E}(K + \varepsilon_1)}{1 + \underline{B}(K + \varepsilon_1) + \underline{C}w} - \underline{D}\Big) \qquad (3.9)$$

approach

$$\frac{(\overline{E} - \underline{B}\,\underline{D})(K + \varepsilon_1) - \underline{D}}{\underline{C}\,\underline{D}}$$

as $t \to \infty$. It follows that for any $\varepsilon_2 > 0$ we can choose $\varepsilon_1 > 0$ sufficiently small so that for some $t_2 > t_1$ we have

$$w_i \le \frac{(\overline{E} - \underline{B}\,\underline{D})(K + \varepsilon_1) - \underline{D}}{\underline{C}\,\underline{D}} + \varepsilon_2$$

provided $t > t_2$. Using $\overline{w}$ defined previously, we have

$$w_i \to\le \overline{w} \ \text{ as } \ t \to \infty \ \text{ for } \ i = 1, 2, \ldots, n.$$

Thus, for any $\varepsilon_3 > 0$ we can choose $\varepsilon_2 > 0$ sufficiently small so that for $t > t_2$ we have

$$\frac{du}{dt} \ \ge \ ru\Big(1 - \frac{u}{K}\Big) - u\Big(\sum_{i=1}^{n} \frac{\overline{A}\overline{w}}{1 + \underline{C}\overline{w}} - \varepsilon_3\Big)$$

$$= \ u\Big(r - \frac{ru}{K} - \frac{n\overline{A}\,\overline{w}}{1 + \underline{C}\overline{w}} - \varepsilon_3\Big). \qquad (3.10)$$

If (3.3) holds and $\varepsilon_3 > 0$ is small then all positive solutions of the logistic equation

$$\frac{du}{dt} = u\Big(r - \frac{ru}{K} - \frac{n\overline{A}\,\overline{w}}{1 + \underline{C}\overline{w}} - \varepsilon_3\Big) \qquad (3.11)$$

approach

$$K\Big[1 - \Big(\frac{n\overline{A}\,\overline{w}}{r(1 + \underline{C}\overline{w})}\Big) - \frac{\varepsilon_3}{r}\Big]$$

as $t \to \infty$. Any solution of (3.10) is bounded below by the solution to (3.11) with the same initial data. Since $\varepsilon_3 > 0$ was arbitrary, we have

$$u \to\ge \underline{u} \equiv K\Big[1 - \Big(\frac{n\overline{A}\,\overline{w}}{r(1 + \underline{C}\overline{w})}\Big)\Big] \ \text{ as } \ t \to \infty$$

so that (3.6) holds for t sufficiently large. Also, for any $\varepsilon_4 \in (0, \underline{u})$ there is a $t_3 > t_2$ such that for $t > t_3$ we have for each i that

$$\frac{dw_i}{dt} \ge w_i\Big(\frac{E(\underline{u} - \varepsilon_4)}{1 + \overline{B}(\underline{u} - \varepsilon_4) + \overline{C}w_i} - \overline{D}\Big). \qquad (3.12)$$

If (3.4) holds and ε_4 is sufficiently small then all positive solutions of

$$\frac{dw}{dt} = w\Big(\frac{E(\underline{u} - \varepsilon_4)}{1 + \overline{B}(\underline{u} - \varepsilon_4) + \overline{C}w} - \overline{D}\Big) \qquad (3.13)$$

approach

$$\frac{(E - \overline{B}\,\overline{D})(\underline{u} - \varepsilon_4) - \overline{D}}{\overline{C}\,\overline{D}} > 0$$

as $t \to \infty$. Since solutions to (3.13) are lower bounds for solutions of (3.12) and since ε_4 is arbitrary, we have

$$w_i \to\ge \frac{(E - \overline{B}\,\overline{D})(\underline{u} - \varepsilon_4) - \overline{D}}{\overline{C}\,\overline{D}}$$

for each i, so that for t sufficiently large (3.7) holds. This completes the proof.

REMARK 3.4. Sharper estimates on the asymptotic behavior of u and $w_1, \ldots, w_n$ could be obtained by making separate estimates for w_i in terms of $A_i, \ldots, E_i$ for each i instead of using the maximum or minimum coefficients. However, the sharper results would also be more complicated.

Theorem 3.2 extends directly to the reaction-diffusion system

$$\frac{\partial u}{\partial t} = d\Delta u + ru\left(1 - \frac{u}{K}\right) - \sum_{i=1}^{n} \frac{A_i u w_i}{1 + B_i u + C_i w_i} \quad \text{on } \Omega,$$

$$\frac{\partial w_i}{\partial t} = d_i \Delta w_i + w_i\left(-D + \frac{E_i u}{1 + B_i u + C_i w_i}\right), \qquad (3.14)$$

$$\frac{\partial u}{\partial \mathbf{n}} = \frac{\partial w_i}{\partial \mathbf{n}} = 0 \qquad \text{on } \partial\Omega, \quad i = 1, 2, \ldots, n$$

where $\Omega \subseteq R^n$ is a bounded domain, Δ denotes the Laplace operator, and $\frac{\partial}{\partial \mathbf{n}}$ denotes the outer normal derivative on $\partial\Omega$. The only modification of the proof is that the comparisons between equations and inequalities which yield the bounds must be justified by comparison principles based on the maximum principle rather than simple differential inequalities.

4. **Discussion.** In systems where there is no intraspecific or interspecific interference but only competition for resources between consumers, the conventional wisdom is that the number of consumer species which can coexist is less than or equal to the number of distinct resources. This has been shown in a number of models, including chemostat models (Smith and Waltman [38]) and the pseudo-equilibrium case of Lotka-Volterra model (MacArthur [31] and Yodzis [42]). In the models which we have considered, the coefficients C_i measure the amount of intraspecific feeding interference that occurs in the ith consumer species. There are several mechanisms which can produce the effect of intraspecific feeding interference. Those include spatial restrictions on where the resource can be exploited and the loss of foraging time due to interactions with conspecifics; see Cosner et al. [11] and the references therein for further discussion. In the case of a single consumer and resource, increasing the coefficient C has the effect of making the consumer density at equilibrium smaller but also stabilizes the equilibrium in some cases; see Cantrell and Cosner [8]. In a sense the phenomenon is like the paradox of enrichment, since the naive assumption would be that reducing intraspecific interference would benefit the consumer by raising the consumer density at equilibrium. In fact, that does occur, but the equilibrium may also lose stability and bifurcate to a limit cycle.

In the case of two consumers, our results indicate that sufficiently strong intraspecific feeding interference of one consumer can not only ensure the long term survival of itself but also guarantee the coexistence of the other consumer which is otherwise out competed. To illustrate numerically, choose $r = 1.5, K = 3, a = 0.45, b = 0.35, d = 0.45, e = 0.55, A = 0.55, B = 0.35, D = 0.45, E = 0.65$, and let C (the intraspecific interference parameter) vary. When $C = 0$, that is, when there is no intraspecific interference, numerical simulations show that the consumer species with density w out competes the consumer species with density v (see Figure 4.1). Introducing intraspecific interference only among the consumer species with density w makes the system coexistent not only in the sense of uniform persistence (Figure
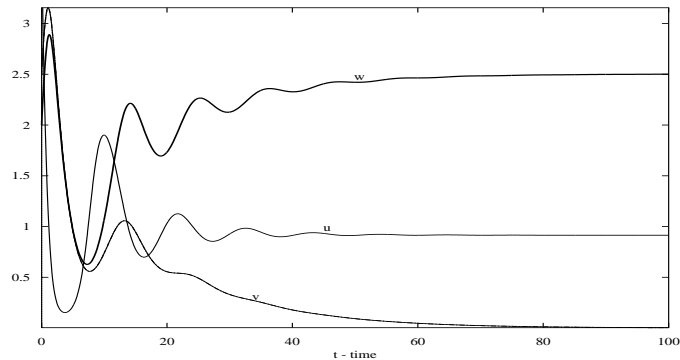
FIGURE 4.1. When $C = 0$, the consumer species with density w wins the competition and the consumer species with density v tends toward extinction.
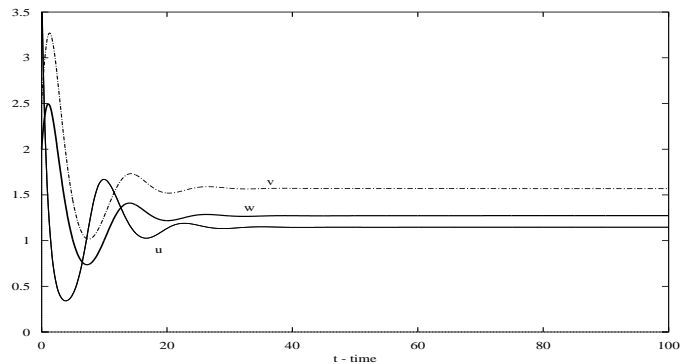

FIGURE 4.2. When $C = 0.2$, both consumer species coexist.

4.2) but also in the sense of global stability (Figure 4.3).   A possible explanation of this phenomenon is that intraspecific feeding interference in one consumer reduces its equilibrium density and allows the other consumer to have better access to the resource. It is also interesting to observe that when the carrying capacity K of the resource is increased in the example, the interior equilibrium loses stability and a three dimensional positive periodic solution arises via Hopf bifurcation. This indicates that the paradox of enrichment phenomenon may occur for the two consumer model as well. However, the three dimensional positive periodic solution can also be regarded as bifurcating from the two dimensional boundary periodic orbit on the $(u, w)-$plane when C increases from 0 to certain positive value (see Figure 4.4).

In the case of many consumers, Theorem 3.2 shows that intraspecific feeding interference can allow coexistence of several consumers on a single resource, but the proof also gives an asymptotic upper bound on consumer densities which gets smaller as the amount of intraspecific interference increases.

Under different conditions on the coefficients the comparison methods we have used here could be used to obtain extinction results. In the present paper our
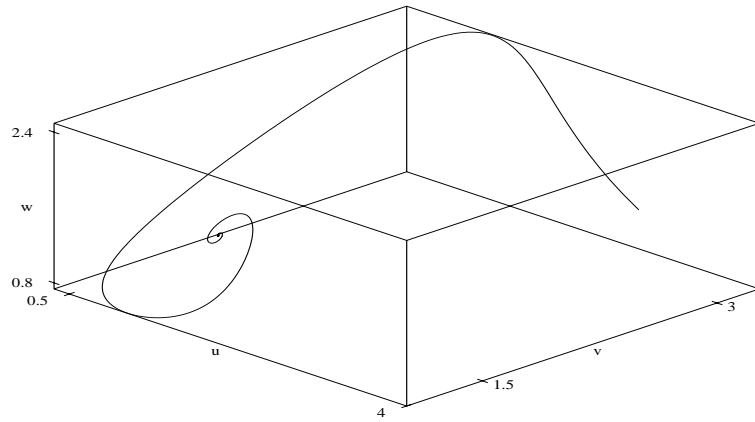
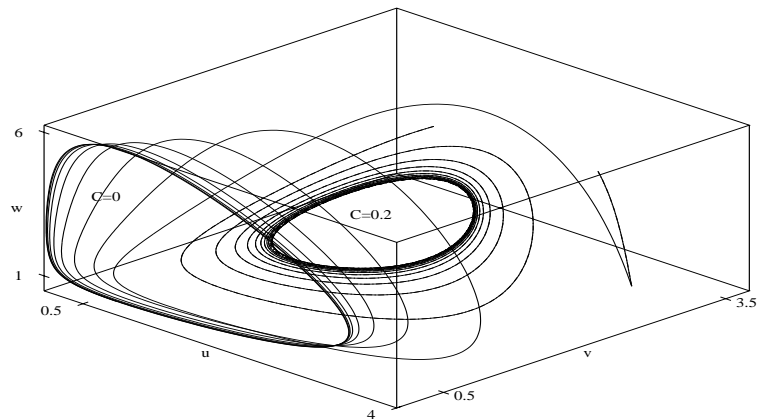FIGURE 4.3. The interior equilibrium is globally stable.

FIGURE 4.4. Choose $K = 6$. When $C = 0$, the two dimensional boundary periodic orbit E_ψ is stable and the consumer species with density v goes extinction. Increasing C to 0.2, a three dimensional positive periodic orbit bifurcates from E_ψ.

interest is to establish that multiple consumers can persist on a single resource, so we will not pursuit the point further.

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