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OSCILLATIONS CAUSED BY CANNIBALISM IN A SIZE-STRUCTURED POPULATION MODEL

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ABSTRACT. A size-structured hierarchical model is derived for the size specific density distribution of a population whose birth, death and growth rates are functions of energy obtained from both cannibalism and alternative food resources. The dynamics of the alternative resources are included in the model. From this integro-partial differential equation model a plane autonomous system is derived for the dynamics of the total population biomass and the alternative resource. When cannibalism is not present it is proved that this system exhibits only global equilibrium dynamics. When cannibalism is included it is shown by examples that sustained oscillations can occur through a Hopf bifurcation to stable limit cycles. This is in contrast to similar models in which the alternative resource is held constant in time.

1. Introduction. Intra-specific predation or cannibalism has important dynamical, evolutionary, and ecological implications for a wide variety of biological organisms, ranging from unicellular organisms to large mammals, and its occurrence is more widespread and frequent than is commonly thought [**7**, **8**, **14**]. Some of the dynamical consequences attributed to cannibalism are population regulation; oscillations in population numbers; age class, size class or life cycle stage dominance; multiple equilibrium states; and hysteresis effects. Mathematical models have been used by several investigators to investigate some of these phenomena; see, for example, [**1**, **2**, **3**, **4**, **5**, **6**, **9**, **10**, **11**, **15**].

Structured models that account for physiological differences between individuals in a population are required for a cannibalism model because the potential of an individual as either a cannibal or a victim depends on certain physiological attributes. One attribute that plays a

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significant factor in cannibalism interactions is body size: cannibals are nearly always larger in size than their victims [**14**]. Most cannibalism models that have been formulated are, however, age-structured. Age, of course, may correlate well with body size. On the other hand, if individual growth rates are dependent upon food resource consumption rates and if cannibalism plays an important role as a food resource then a more accurate model must be built using body size as the structuring variable. Unfortunately, size-structured models are generally more complicated to analyze than age-structured models, particularly if individual growth rates are density and/or size dependent.

One class of structured models that are both analytically tractable and capable of being applied to cannibalism interactions are those termed "hierarchical" in [**5**] (also see [**4**]). These are model equations that are built upon the assumption that interactions between individuals in a population that affect birth, death and growth rates are based upon a hierarchy in age or size in such a way that an individual's vital rates are dependent upon the density of all other individuals either higher or lower in the hierarchy, i.e., all individuals who are either younger or older (in an age hierarchical population) or smaller or larger (in a body size hierarchical population). While certainly not able to model fine details of intraspecific interactions between individuals, these kinds of models can qualitatively capture the essential features of such an interaction that drive the dynamics of the population. If "simpler" models of cannibalism can account for dynamical phenomena such as those listed above, then not only can it be expected that more complicated and detailed models of cannibalism will also exhibit these features, but it can then be argued that these dynamical phenomena are fundamental consequences of cannibalism. (For a discussion of the importance of hierarchies with regard to food resource intraspecific competition, as opposed to intraspecific predation, see [**12**].)

In [**4**] a size-structured hierarchical model for cannibalism is derived and studied. Despite the complexity and generality of the integro-partial differential equations involved in the model, it is shown in [**4**] that only equilibrium dynamics are possible and consequently these kinds of models cannot account for sustained oscillations as a dynamical feature of cannibalism. The general model derived in [**4**], however, assumes that alternative food resources (i.e., resources not obtained by cannibalism) are held fixed in time at a constant level. (Indeed, all models in the literature of which we are aware make this assumption.) If alternative resources change in time, either because of consumption by the population itself or because of external fluctuations in the environment (such as seasonality), then a more accurate model would take the dynamics of these resources into account. This is important because the intensity of cannibalism is usually inversely related to the availability of alternative food resources [**14**].

Our goal in this note is to show that a size-structured hierarchical model such as considered in [**4**] can predict sustained population oscillations if it is modified to allow for the dynamics of alternative food resources.

In Section 2 the size-structured model is described and in Section 3 it is shown how the model can be reduced to a plane autonomous system of ordinary differential equations. In order to argue that it is cannibalism that cause the sustained oscillations, we analyze the model in the absence of cannibalism in Section 4. There the non-cannibalism model is proved always to have a globally stable equilibrium and hence cannot exhibit sustained oscillations. Because of its complexity, the full cannibalism model is not studied here, but in Section 5 we show numerically by means of an example that when cannibalism is included sustained oscillations can occur through a classical Hopf bifurcation to a stable limit cycle.

2. Model description. Let $\rho(t,s)$ be the population density where t denotes time and s denotes body size, namely biomass (or volume). Then the dynamics of ρ are governed by the equation

$$\partial_t\rho + \partial_s(g\rho) = -d\rho, \qquad t > 0,\ s > s_b, \tag{1}$$

$$g\rho|_{s=s_b} = \int_{s_b}^{s_m} b\rho(t,\sigma)\,d\sigma, \qquad t > 0, \tag{2}$$

where d is the death rate, b is the birth rate, and g is the growth rate of individuals (biomass per unit time) [**13**]. Here we have assumed that all newborns have the same biomass $s_b > 0$ and that there is a maximal body biomass $s_m \in (s_b, +\infty]$ at which growth stops. Thus, we assume that the rate of growth of the total biomass of individuals of size s_m is zero:

$$g\rho(t,s)|_{s=s_m} = 0, \qquad \forall t \geq 0.$$

Following [**15**], we assume that growth and fertility rates of an individual of biomass s are proportional to the resource energy uptake rate $E = E_c + E_o$ per unit biomass, where E_c denotes the uptake rate of energy obtained from cannibalism and E_o denotes the uptake rate of energy from other sources. Thus, we write

$$g = \gamma(E_c + E_o)s, \qquad b = \beta(E_c + E_o)s$$

where $\gamma > 0$ and $\beta > 0$ are conversion and allocation factors from energy to growth and reproduction, respectively. The death rate is broken into two components $d = d_c + d_o$, where d_c is the death rate of individuals of size s due to cannibalism and d_o is that due to other causes.

For simplicity, in this paper we assume that E_o is proportional to the amount $R = R(t)$ of non-cannibalistic food resources available per unit time, so that

$$E_o = uR, \qquad u > 0.$$

We assume that the only possible victims for a cannibal of size s are individuals of equal or smaller size. Therefore, the energy uptake rate E_c from cannibalism by an individual of size s will be taken as a function of the size (total biomass) of the sub-population of individuals smaller in size than s, i.e., of the quantity

$$S(t,s) = \int_{s_b}^{s} \sigma\rho(t,\sigma)\,d\sigma.$$

In this paper we will make the simple assumption that E_c for an individual of size s is proportional to $S(t,s)$ or $E_c = cS(t,s)$. Furthermore, we want to account for the fact that the intensity of cannibalism is usually inversely related to the availability of alternative food resources [**14**]. Therefore, we assume that the "cannibalism coefficient" $c = c(R)$ is a decreasing function of R and write

$$E_c = c(R)S(t,s),$$

where

$$c : (-\infty, +\infty) \to [0, +\infty) \tag{3}$$

is continuously differentiable and

$$c'(R) \leq 0 \qquad \text{for all } R > 0.$$

The death rate $d_o = d_o(E)$ is assumed to be a function of the individual's total energy uptake rate E, decreasing from a "starvation" death rate d_s when E is zero to a minimal "natural" death rate d_m as E increases without bound, as described in the conditions

$$\begin{aligned} d_o : (-\infty, +\infty) \to [0, +\infty) \quad & \text{is continuously differentiable,} \\ d_o'(E) \leq 0 \quad & \text{for all } E > 0, \\ d_o(0) \doteq d_s > d_m \doteq d_o(+\infty) > 0. & \end{aligned} \tag{4}$$

By assumption, the threat of cannibalism to an individual of size s comes only from individuals of equal or larger size. Therefore, we assume that the death rate due to cannibalism d_c depends on the size (total biomass) of the sub-population of individuals of equal or larger size, i.e., on the quantity

$$L(t,s) = \int_s^{s_m} \sigma\rho(t,\sigma)\,d\sigma.$$

Specifically, in this paper we will take the death rate d_c to be proportional to $L(t,s)$, so that $d_c = \delta L(t,s)$. However, since in our model the intensity of cannibalism is inversely related to the amount of other resources available, we assume that the coefficient $\delta = \delta(R)$ is a decreasing function of R. Thus, we write

$$d_c = \delta(R)L(t,s),$$

where

$$\begin{aligned} \delta : (-\infty, +\infty) \to [0, +\infty) \quad & \text{is continuously differentiable and} \\ \delta'(R) \leq 0 \quad & \text{for all } R > 0. \end{aligned} \tag{5}$$

In summary, equations (1)–(2) become

$$\partial_t \rho + \partial_s(\gamma E(R,S) s\rho) = -d(R,S,L)\rho, \tag{6}$$

$$\gamma E(R,S)s\rho|_{s=s_b} = \int_{s_b}^{s_m} \beta E(R,S)\sigma\rho(t,\sigma)\,d\sigma, \tag{7}$$

where

$$\begin{aligned} d(R,S,L) &= d_o(E(R,S)) + \delta(R)L, \\ E(R,S) &= uR + c(R)S. \end{aligned}$$

If the resource R is held constant, then this model reduces to the one studied in [4]. Here we wish to consider a dynamically varying resource R in order to capture the important feature of cannibalism that the rate of cannibalism is a decreasing function of R. We will consider the case when, in the absence of the population, the resource has a unique positive equilibrium and this equilibrium is stable. Specifically, the dynamics of $R = R(t)$ will be assumed to be governed by a scalar equation

$$R' = f(R)$$

where the function f satisfies the conditions

$$\begin{gathered} f : (-\infty, +\infty) \to (-\infty, +\infty) \quad \text{is continuously differentiable,} \\ \text{either} \quad f(0) > 0 \text{ or } f(0) = 0 \quad \text{and} \quad f'(0) > 0, \\ \text{there exists a unique positive } K > 0 \text{ such that } f(K) = 0, \\ f'(K) < 0, \qquad Rf'(R) < f(R) \quad \forall R > 0. \end{gathered} \tag{8}$$

Two prototypical examples are

$$f = r(K - R), \qquad f = r(1 - R/K)R.$$

In the presence of the cannibalistic population, the dynamics of R are given by the equation

$$R' = f(R) - uRB. \tag{9}$$

Suppose, for simplicity, that the resource units are chosen so that $K = 1$. Here

$$B(t) = \int_{s_b}^{s_m} \sigma\rho(t,\sigma)\,d\sigma$$

is the total biomass of the population.

3. Model simplification. The analysis of nonlinear integro-differential equations such as (6)–(7)–(9) is difficult in general. Our specific equation, however, has the form of what is called a "hierarchical" equation in [**5**]. For this kind of equation it is possible to obtain a more tractable ordinary differential equation for the total biomass $B(t)$. We will give a heuristic derivation of this equation. A rigorous derivation will appear in [**16**].

Multiplying (6) by s, integrating from s_b to s_m, we obtain the equation

$$B'(t) = \int_{s_b}^{s_m} ((s_b\beta + \gamma)E(R,S) - d(R,S,L))\sigma\rho(t,\sigma)\,d\sigma.$$

Noting that, for any $t > 0$,

$$\frac{\partial S}{\partial s} = s\rho, \qquad L = B - S,$$

we write

$$B'(t) = \int_{s_b}^{s_m} ((s_b\beta + \gamma)E(R,S) - d(R,S,B-S))\frac{\partial S}{\partial \sigma}\,d\sigma.$$

The change of variable from s to $z = S(t,s)$ (for fixed $t > 0$) in the integral yields the ordinary differential equation

$$B'(t) = \int_{0}^{B(t)} ((s_b\beta + \gamma)E(R(t),z) - d(R(t),z,B(t)-z))\,dz$$

or

$$B' = \left((s_b\beta + \gamma)uR + \frac{1}{2}((s_b\beta + \gamma)c(R) - \delta(R))B\right)B - \int_0^B d_o(uR + c(R)z)\,dz$$

for the total population biomass $B = B(t)$.

This equation and the equation (9) define a plane autonomous system of ordinary differential equations for $R = R(t)$ and $B = B(t)$.

If the resource is held at its inherent equilibrium level, i.e., $R \equiv 1$, then $uR = u$ is the amount of resource consumed by a unit of biomass per unit time. In the absence of cannibalism ($c(R) \equiv \delta(R) \equiv 0$), the expected life space of a unit of biomass is $1/d_o(u)$. Thus, $r \doteq u/d_o(u)$ is the expected amount of resource consumed by a unit of biomass during its life, $s_b\beta r$ is the amount of biomass contributed by a unit of biomass to the population by reproduction, and γr is the amount of biomass contributed to the population by growth. Therefore, the quantity

$$n \doteq s_b\beta r + \gamma r = (s_b\beta + \gamma)\frac{u}{d_o(u)}$$

is the total biomass contributed by a unit of biomass to the population during its life, provided cannibalism is absent and the resource is held at its equilibrium $K = 1$. We call n the "*inherent net reproductive number.*"

If we introduce n into the model equations, then we have, finally, the following plane autonomous system of equations for the dynamics of the resource level R and the total population biomass B:

$$\begin{aligned} R'(t) &= f(R) - uRB, \\ B'(t) &= \left(nd_o(u)R + \frac{1}{2}\left(\frac{nd_o(u)}{u}c(R) - \delta(R)\right)B\right)B \\ &\qquad - \int_0^B d_o(uR + c(R)z)\,dz. \end{aligned} \tag{10}$$

4. Dynamics in the absence of cannibalism.

We begin by studying the plane autonomous system (10) when cannibalism is absent. From an understanding of the dynamics in this case we can see, by comparison, the effects on the dynamics of the population when cannibalism is present.

In the absence of cannibalism ($c = \delta = 0$), the dynamics of the interaction between the population and the resource are governed by the plane autonomous system

$$\begin{aligned} R' &= f(R) - uRB, \\ B' &= (nd_o(u)R - d_o(uR))B. \end{aligned} \tag{11}$$

It is not difficult to show that the positive quadrant is forward invariant under the flow defined by (11). The global asymptotic dynamics in the positive quadrant are described in the following result.

Theorem 1. *Assume* (4) *and* (8) *and let* $(R(t), B(t))$ *be a solution of* (11) *with* $(R(0), B(0)) > 0$. *Then*

$$n < 1 \Longrightarrow \lim_{t \to +\infty} (R(t), B(t)) = (1, 0),$$
$$n > 1 \Longrightarrow \lim_{t \to +\infty} (R(t), B(t)) = (R_o, B_o) > 0,$$

where (R_o, B_o) *is the unique positive equilibrium.*

The proof of this theorem is given in the Appendix.

One way to understand this theorem is to view it in terms of bifurcating equilibria. The "trivial" equilibrium $(R, B) = (1, 0)$ exists for all values of the inherent net reproductive number $n > 0$. This equilibrium is stable until it loses its stability as n is increased through the critical value $n = 1$ at which point a branch of stable positive equilibrium bifurcates from the trivial equilibrium and exists for $n > 1$. This is a typical "stable" or "supercritical" bifurcation or a "bifurcation to the right."

This theorem tells us that, in the absence of cannibalism, our model population equilibrates, and in particular can exhibit no sustained oscillations. It also says that the population can survive if and only if its inherent net reproductive number n is greater than 1, that is to say, if and only if each unit of biomass is expected over the course of its life to do better than just replace itself when population density is low.

5. Stable limit cycles due to cannibalism. We will show in this section by numerical examples that cannibalism can cause sustained oscillations to occur. This will be done by demonstrating that a Hopf bifurcation to a stable limit cycle can occur for the plane autonomous system (10), unlike for the similar size-structured hierarchical model in [**5**] in which resource dynamics are excluded.

The expressions

$$c(R) = \frac{c_o}{1 + c_1 R}, \qquad \delta(R) = \frac{\delta_o}{1 + \delta_1 R}$$
$$d_o(E) = d_m + (d_s - d_m)e^{-aE}, \tag{12}$$

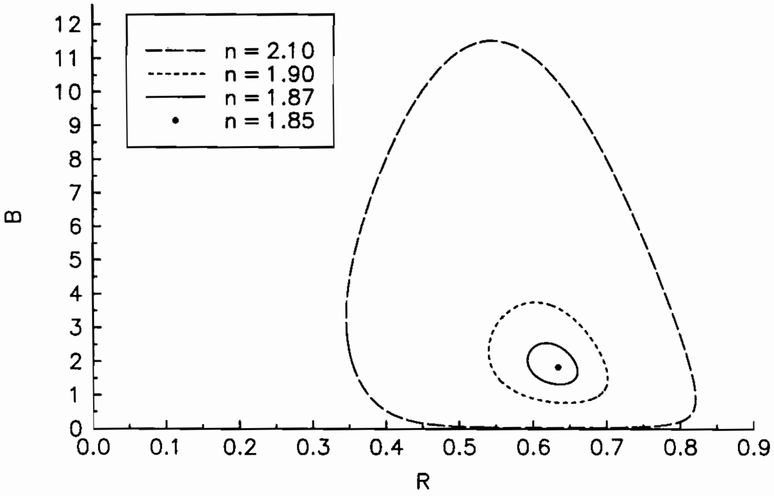

FIGURE 1. A stable equilibrium and three stable limit cycles are shown as the value of the inherent net reproductive number n is increased through a Hopf bifurcation value somewhere between 1.85 and 1.87. These graphs were computed from the system (10) with (12) and $f(R) = \rho R(1-R)$. The values of the coefficients are $\rho = 0.5$, $u = 0.1$, $c_o = 1.0$, $c_1 = 30.0$, $\delta_o = 100.0$, $\delta_1 = 30.0$, $d_m = 1.0$, $d_s = 10.0$, $a = 10.0$.

and

$$f(R) = \rho R(1-R) \quad \text{or} \quad \rho(1-R),$$

in which all of the coefficients are nonnegative and $d_s > d_m \geq 0$ satisfy all of the requirements (3), (5), (4) and (8).

Theorem 1 implies only equilibrium dynamics occur if $c_o = \delta_o = 0$ (no cannibalism is present).

When these coefficients are positive, however, limit cycles can occur as is shown in Figure 1 for the logistic case $f(R) = \rho R(1-R)$ and in Figure 2 for the case $\rho(1-R)$. In these figures a small amplitude, stable limit cycle is shown emerging from an equilibrium as n increases through a critical value at which the equilibrium loses its stability.

6. Concluding remarks. We have derived a size-structured, hierarchical model for the dynamics of the density distribution of a popu-

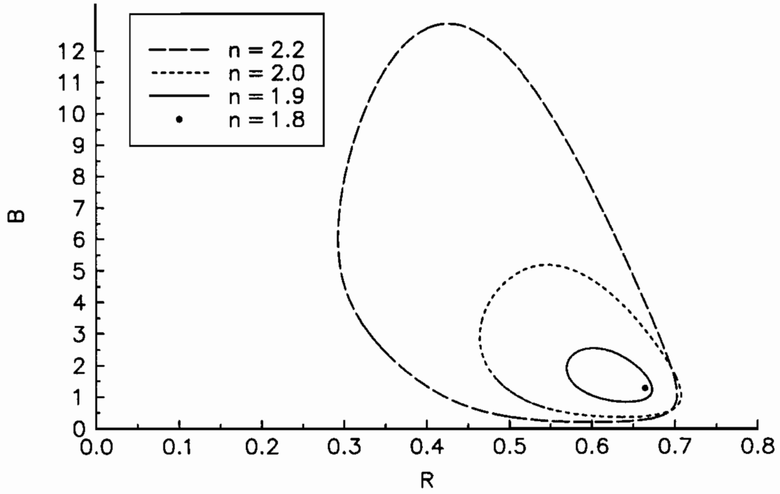

FIGURE 2. A stable equilibrium and three stable limit cycles are shown as the value of the inherent net reproductive number n is increased through a Hopf bifurcation value somewhere between 1.8 and 1.9. These graphs were computed from the system (10) with (12) and $f(R) = \rho(1-R)$. The values of the coefficients are $\rho = 0.25$, $u = 0.1$, $c_o = 1.0$, $c_1 = 30.0$, $\delta_o = 100.0$, $\delta_1 = 30.0$, $d_m = 1.0$, $d_s = 10.0$, $a = 10.0$.

lation that obtains energy from both cannibalism and alternative food resources. The dynamics of the alternative food resources are dynamically modeled and it is assumed that the intensity of cannibalism is a decreasing function of the amount of alternative resources available at any given time. The model assumes that the energy obtained from cannibalism by any individual is a function of (specifically, is proportional to) the size of the sub-population of individuals of smaller size. This assumption, and the assumption that the death rate due to cannibalism is a function of the sub-population of individuals of larger size, is made in order to qualitatively capture the observed biological fact that usually cannibals are larger in body size than their victims. Mathematically, this assumption allows us to derive a scalar ordinary differential equation for the dynamics of total population biomass from the complicated integro-partial differential equations (6)–(7) of the size-structured model. By including the dynamics of the alternative resource, the more analytically tractable plane autonomous system (10) is obtained for the dynamics of both the resource and the total biomass of the population.

It is proved that in the absence of cannibalism the resource and the model population exhibit only global equilibrium dynamics. However, it is shown that in the presence of cannibalism sustained oscillations can occur through a Hopf bifurcation to stable limit cycles. No rigorous proof of the Hopf bifurcation is given, but instead its possibility is only demonstrated numerically for typical examples.

The existence of sustained oscillations in the cannibalism model is in contrast to similar size-structured cannibalism models in which the alternative food resource is held at a constant level and only equilibrium dynamics occur. Thus, at least in these kinds of models, for sustained oscillations to occur it is necessary that the alternative food resource be allowed to vary in time, in order to capture in the model the full effect of the fact that the intensity of cannibalism is inversely related to the availability of alternative food sources.

Since the goal of this note was a simple demonstration that cannibalism can be the source of oscillations, we have not attempted to derive and analyze the most general possible model nor models that might be considered more "realistic." Thus, the simplest kind of Lotka-Volterra interaction terms and resource uptake terms were used (and nonlinear functions were assumed defined globally). The fact that simpler models can imply sustained oscillations in the presence of cannibalism serves to make our point more forcibly, we feel, than would more complicated models. This is especially true if the models have no possibility for sustained oscillations in the absence of cannibalism. For example, Holling II functional responses could have been used instead of Lotka-Volterra type responses. In such a model, however, there would have been the possibility of sustained oscillations in the absence of cannibalism (when f is logistic), unlike the model based on Lotka-Volterra responses.

APPENDIX

Lemma 1. *System* (11) *has a positive equilibrium if and only if* $n > 1$ (*in which case it is unique*). *If* $f(0) > 0$, *then the only other nonnegative equilibrium is* $(R, B) = (1, 0)$. *If* $f(0) = 0$, *then the only other nonnegative equilibria are* $(R, B) = (1, 0)$ *and* $(0, 0)$.

Proof. From (11), it is easy to see that positive equilibria $(R, B) = (R_o, B_o)$ are given by

$$B_o = \frac{f(R_o)}{uR_o},$$

where $R = R_o > 0$ is a positive root of the equation

$$g(R) \doteq nRd_o(u) - d_o(uR) = 0$$

that satisfies $R_o < 1$. It is necessary that $R_o < 1$ because (8) implies that $f(R) < 0$ for $R > 1 = K$ and hence a root of $g(R)$ satisfying $R_o \geq 1$ would imply that $B_o = f(R_o)/uR_o \leq 0$. Thus, (11) has a positive equilibrium if and only if $g(R)$ has a root on the open unit interval $(0, 1)$. By (4), $g'(R) = nd_o(u) - ud'_o(uR) > 0$ and $g(0) = -d_s < 0$. It follows that $g(R)$ has a root on $(0, 1)$ if and only if $g(1) = (n - 1)d_o(u) > 0$, i.e., if and only if $n > 1$. Since $g(R)$ is strictly increasing on $(0, 1)$ this root is unique when it exists.

We have left only the possibility of equilibria on the boundary of the positive quadrant. It is easy to see from the second equation in (11) that there cannot be an equilibrium on the positive B-axis. It follows from (8) that the only equilibrium on the positive R-axis is $(1, 0)$. Finally, the origin is easily seen to be an equilibrium if and only if $f(0) = 0$. □

Lemma 2. *The equilibrium* $(R, B) = (1, 0)$ *of* (11) *is locally asymptotically stable if* $n < 1$ *and is a saddle if* $n > 1$. *In the latter case, the positive* R*-axis is the stable manifold of* $(1, 0)$ *and no orbit lying in the positive quadrant can have* $(1, 0)$ *as an* ω*-limit point.*

Proof. The Jacobian at (1,0) is given by

$$J = \begin{pmatrix} f'(1) & -u \\ 0 & (n-1)d_o(u) \end{pmatrix}.$$

It follows from assumptions (8) that the eigenvalue $f'(1) < 0$. The remaining eigenvalue $(n - 1)d_o(u)$ has the sign of $n - 1$. Therefore,

$$n > 1 \Longrightarrow (1, 0) \text{ is unstable,}$$
$$n < 1 \Longrightarrow (1, 0) \text{ is locally asymptotically stable.}$$

In both cases the R-axis is the stable manifold. Thus, in the unstable case when $n < 1$, no orbit in the positive quadrant can have (1,0) as an ω-limit point (by the Hartman-Grobman theorem). □

Lemma 3. *Suppose that* $f(0) = 0$. *Then the equilibrium* $(R, B) = (0,0)$ *of* (11) *is a saddle. Moreover, the positive* R*-axis lies in its unstable manifold while the positive* B*-axis lies in its stable manifold and no orbit lying in the positive quadrant can have* $(0,0)$ *as an* ω*-limit point.*

Proof. The Jacobian at the origin is

$$J = \begin{pmatrix} f'(0) & 0 \\ 0 & -d_s \end{pmatrix}.$$

Since $f'(0) > 0$ by assumption (8), the origin is a saddle. Moreover, since in this case they are invariant, the coordinate axes are the stable and unstable manifolds of this saddle point. It follows by the Hartman-Grobman theorem that no orbit in the positive quadrant can have the origin in its ω-limit set. □

Lemma 4. *The positive quadrant is forward invariant under the flow defined by* (11).

Proof. Clearly the R-axis is invariant under (11). If $f(0) = 0$, then the B-axis is also invariant. If $f(0) > 0$, then it is easy to see from the direction field defined by (11) that the flow along the B-axis points in to the positive quadrant. Thus, in either case, no orbit in the positive quadrant at any time can ever leave the positive quadrant at a later time. □

Lemma 5. *Any orbit defined by* (11) *with initial conditions* $(R(0), B(0))$ *lying in the positive quadrant is bounded for all* $t \geq 0$.

Proof. Forward boundedness will follow if we can show the existence of a polygonal region in the (R, B)-plane of the kind shown in Figure 3 which contains the initial point and from which the orbit cannot escape for $t \geq 0$. We construct such a polygon as follows.

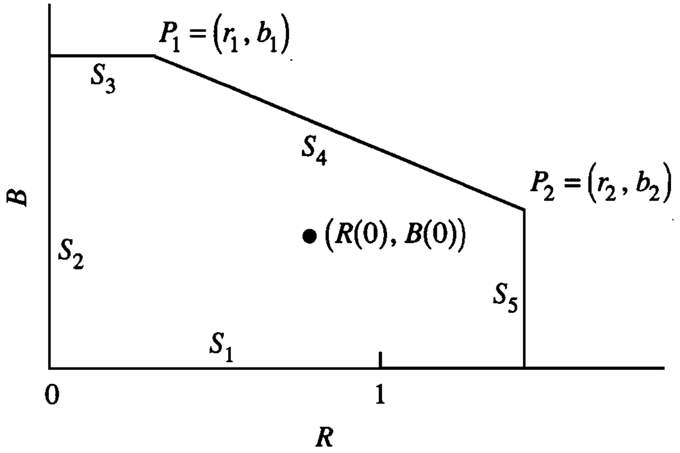

FIGURE 3. The polygon in the phase plane of system (10) that is used in the proof of Lemma 5 is shown.

By (4) there exists a small positive number $r_1 \in (0,1)$ such that

$$uRd_o(u) - d_o(uR) < 0, \qquad R \in [0, r_1]. \tag{13}$$

Pick any real

$$r_2 > \max\{1, R(0)\} \tag{14}$$

and any positive real

$$m > \frac{ud_o(u)r_2 - d_o(ur_2)}{ur_2}. \tag{15}$$

This will guarantee that

$$\kappa_1(R) \doteq -muR + ud_o(u)R - d_u(uR) < 0$$

and that $\kappa_1(R)$ is bounded away from 0 as a function of $R \in [r_1, r_2]$. Then, since the expression

$$\kappa_2(R) \doteq mf(R) - m(R - r_2)\kappa_1(R)$$

is bounded on this same interval $R \in [r_1, r_2]$ it is possible to choose $b_2 > B(0)$ so large that

$$\kappa_1(R)b_2 + \kappa_2(R) < 0 \tag{16}$$

on this interval.

We now construct the polygon in Figure 3 giving the corner P_2 the coordinates (r_2, b_2) and defining the linear side S_4 between P_1 and P_2 to be given by the linear equation

$$B = -m(R - r_2) + b_2.$$

The point P_1 then has coordinates (r_1, b_1) where $b_1 = -m(r_1 - r_2) + b_2$.

Having specified the polygon in Figure 3 in this manner, we now show that the flow defined by (11) cannot leave this polygon. We do this by investigating the direction field on each of the five sides.

No orbit can leave the polygon across the bottom side S_1 or the left vertical side S_2 by Lemma 4. No orbit can leave the polygon across the vertical right side S_5 since by (14) the derivative $R' < 0$ along this side. No orbit can leave the polygon across the horizontal top side S_3 since by (13) the derivative $B' < 0$ along this side.

We have left to consider the linear side S_4. No orbit can leave across this final side of the polygon if the direction field defined by (11) points inward along this side. This will be true if the inner product of the direction field vector (f_1, f_2) with the externally pointing normal $(m, 1)$ to this side is negative. A straightforward calculation shows this inner product to be $\kappa_1(R)b_2 + \kappa_2(R)$, which by (16) is indeed negative along S_4 because $R \in [r_1, r_2]$ along this side. □

Lemma 6. *The plane autonomous system* (11) *can have no limit cycles in the positive quadrant.*

Proof. We use the Dulac principle. The divergence of the flow defined by (11) multiplied by $1/RB$ is

$$\frac{\partial}{\partial R}\left(\frac{R'}{RB}\right) + \frac{\partial}{\partial B}\left(\frac{B'}{RB}\right) = \frac{Rf'(R) - f(R)}{R^2 B}$$

which is negative (hence nonzero) in the positive quadrant by (8). □

Proof of Theorem 1. We consider two cases.

Case 1. Suppose that $n < 1$. By Lemma 1 there exists no equilibria in the positive quadrant. By Lemma 6 there are also no limit cycles in the positive quadrant. Since orbits starting in the positive quadrant remain there and are bounded for all $t \geq 0$ (Lemmas 4 and 5) it follows by the Poincare-Bendixson theorem that the ω-limit set Ω must lie on the nonnegative axes.

Consider first the B-axis. If $f(0) > 0$, then the flow along this axis is into the polygon and hence no point on this axis can lie in Ω. If $f(0) = 0$, then the origin is an equilibrium with the positive B-axis as its stable manifold. By the invariance and closure of Ω, if a point on the positive B-axis lay in Ω, then so must the origin, in contradiction to Lemma 3.

We conclude that Ω lies on the positive R-axis. Since the equilibrium (1,0) is a global attractor on the positive R-axis, it follows by the closure and invariance of Ω that $(1, 0)$ must lie in Ω. However, because $n < 1$ the equilibrium $(1, 0)$ is locally asymptotically stable and hence Ω must consist solely of this point.

Case 2. Suppose $n > 1$. In this case there exists, by Lemma 1, a unique positive equilibrium $(R_o, B_o) > 0$. By Lemma 2, the equilibrium (1,0) cannot lie in Ω. Arguing exactly as in Case 1, we know then that no point on the boundary of the positive quadrant can lie in Ω. It now follows from Lemmas 4, 5 and 6 and from the Poincare-Bendixson theorem that Ω consists solely of the equilibrium (R_o, B_o). □

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