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Cannibalism Can Be Beneficial Even When Its Mean Yield Is Less than One

Shandelle M. Henson

Department of Mathematics, University of Arizona, Tucson, Arizona 85721

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Two types of adult-on-juvenile cannibalism are discussed and differentiated: those with "mean yield of cannibalism" greater than one, and those with mean yield less than one. Two extant models—one continuous and one discrete—in which cannibalism is beneficial only when the mean yield exceeds one are reviewed and compared. The discrete model is modified and analyzed to demonstrate that cannibalism can be beneficial even when the mean yield is *less* than one. © 1997 Academic Press

1. INTRODUCTION

Cannibalism occurs in many contexts across a wide spectrum of taxa [6–8, 17]. Several models in the literature have demonstrated circumstances under which cannibalism can enable a population to remain viable when it would otherwise become extinct [1–5, 9–11, 13, 16, 18].

Some models, e.g. [2, 18], have been used to demonstrate the beneficial results of adult-on-juvenile cannibalism when juveniles have access to a (constant) resource *unavailable* to adults. When adult resource is too low to support a noncannibalistic population, the adults can indirectly utilize this extra resource through cannibalized juveniles.

On the other hand, biologists believe cannibalism can also be beneficial if adults and juveniles utilize the *same* (variable) resource [7]. In this case cannibalism can be used by adults during times of low resource to redirect reproductive effort until a time of higher resource. Although these two modes of cannibalism by no means exhaust the ways in which cannibalism can benefit a population, the focus of this paper is on these two types. Two models of the first type of cannibalism will be reviewed, and a model of the second type will be presented.

First, however, we need a modelling concept which can differentiate between these two modes of cannibalism. We find such a concept in the work of Van den Bosch *et al.* [18]. They define the *mean yield* of cannibalism to be the expected number of new juveniles produced due to the cannibalization of one juvenile at low population density. The mean yield is the number of new juveniles which arise from and replace one cannibalized juvenile. In general the mean yield depends on parameters and submodels such as juvenile and adult resource levels, juvenile and adult survivorships in the absence of cannibalism, the expected energetic content of a juvenile, and energy-to-offspring conversion factors.

If juveniles utilize a resource unavailable to adults, then the mean yield at low (adult) resource levels can exceed one because of this extra energy source. If, on the other hand, juveniles and adults utilize the same resource, then the mean yield must be less than one at low resource levels by energetic considerations. In particular, if in a given model juveniles and adults utilize the same resource and the mean yield is independent of resource level (as it is for the sake of simplicity in many models), then the model parameters should be such that the mean yield is less than one; otherwise at zero resource level cannibalism could create a perpetual motion machine.

This paper (1) clarifies the usefulness of the concept of mean yield in modelling cannibalistic populations; (2) reviews a continuous model and a discrete model in which cannibalism is beneficial only when the mean yield exceeds one; and (3) modifies the discrete model by

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means of a variable resource and demonstrates cannibalism can be beneficial even if the mean yield is less than one.

2. MEAN YIELD IN THE VAN DEN BOSCH ET AL. AND CUSHING MODELS

Van den Bosch *et al.* [18] analyzed a continuous age structured adult-on-juvenile cannibalism model with constant resource in which the mean yield was allowed to exceed one. They showed that a branch of positive equilibria bifurcates from the trivial (zero) equilibrium at inherent net reproductive number $r = 1$. The trivial solution is locally stable for $r < 1$ and unstable for $r > 1$. They furthermore showed that the branch bifurcates subcritically exactly when

$$\zeta\psi + \zeta Z\left(\frac{-\psi f'(Z)}{f(Z)}\right) > 1,$$

where ζ, ψ, and Z represent the conversion efficiency of ingested energy to the production of new juveniles, the expected energy gain from cannibalizing one juvenile at low adult density, and the rate of energy intake per adult of extraneous (adult) resource, respectively. ψ depends on the cannibalization preference distribution, the juvenile energy content distribution, and the juvenile survivorship. $-\psi f'(Z)/f(Z)$ can be interpreted as the expected increase in adult lifespan due to one cannibalization, where f is the per capita adult death rate with $f'(Z) < 0$. They defined the mean yield to be

$$\zeta\psi + \zeta Z\left(\frac{-\psi f'(Z)}{f(Z)}\right),$$

the sum of the new juveniles immediately resulting from one cannibalization and the new juveniles resulting from consumption of extraneous (adult) resource during the additional time lived by the cannibal.

Therefore, van den Bosch *et al.* concluded that the branch of equilibria bifurcates subcritically exactly when the number of new juveniles resulting from the cannibalization of one juvenile exceeds one (i.e., when the mean yield exceeds one). In some cases the branch bends back to the right, affording (expectedly stable) equilibria for the cannibalism model in the region $r < 1$ where noncannibals cannot survive. Thus cannibalism can allow the population to survive when it would otherwise go extinct. This benefit of cannibalism occurs, however, only when the mean yield exceeds one.

Cushing [2] analyzed the dynamics of a discrete adult-on-juvenile cannibal model with constant resource. Although Cushing did not describe the dynamics in terms of mean yield, his results admit comparison with those of van den Bosch *et al.*. The scaled version of the model he analyzed is:

$$J(t+1) = r\left[f(A(t)) + \frac{c}{\rho}\,\psi(A(t))\,\Phi(J(t))\right]A(t)$$

$$A(t+1) = [1 - c\Psi(A(t))\,\phi(J(t))]\,J(t)$$

where

$$\Phi(J) \doteq \phi(J)\,J, \quad \Psi(A) \doteq \psi(A)\,pA$$

$$0 \leqslant f(A) \leqslant 1, \quad f(0) = 1, \quad f'(A) < 0, \quad f(\infty) = 0$$

$$0 \leqslant \phi(J) \leqslant 1, \quad \phi(0) = 1, \quad \phi'(J) < 0,$$

$$\Phi'(J) > 0, \quad \Phi(\infty) < \infty$$

$$0 \leqslant \Psi(A) \leqslant 1, \quad \Psi(0) = 0, \quad \Psi'(A) > 0, \quad \Psi(\infty) = 1.$$

$r = p\zeta e_j\rho$ is the inherent net reproductive number, where p, ζ, e_j, and ρ are the probability that a juvenile will mature in the absence of cannibalism, the energy-to-new juvenile conversion factor, the average energetic content of a juvenile, and the resource level, respectively. The coefficient c indicates the strength of the cannibalism interaction, $f(A)$ represents the fractional decrease in resource consumption per adult due to intraspecific competition, and $c\Psi(A)\,\phi(J)$ is the probability that a juvenile will be cannibalized when the population consists of pA adults and J juveniles. Cushing showed that, in the absence of cannibalism ($c = 0$), a branch of locally stable positive equilibria bifurcates supercritically from the trivial solution at $r = 1$. At low resource levels the introduction of cannibalism can increase the equilibrium levels and thus raise the bifurcating branch; this can be considered a benefit of cannibalism. Numerical simulations gave examples where further increases in the degree of cannibalism cause the bifurcating branch to become subcritical and "bend over," resulting in an unstable lower branch and stable upper branch. In this case, cannibalism can allow the population model to equilibrate in a parameter region to the left of the bifurcation point (where in the absence of cannibalism the population cannot exist). This is another manifested benefit of cannibalism in Cushing's model. Under what conditions on the mean yield do these benefits occur?

Cushing showed that the condition for subcritical bifurcation is (with corrected typographical error)

$$\left(1-\frac{1}{\rho p}\right)c\Psi'(0)-f'(0)<0$$

which can be written as

$$\zeta e_j > 1-\frac{f'(0)}{c\Psi'(0)}.$$

In order to compare Cushing's results with those of van den Bosch *et al.*, note that the analogous "mean yield" in this model is ζe_j. The condition for subcritical bifurcation in Cushing's model differs from that in the van den Bosch *et al.* model for three reasons. First, the density dependence in the recruitment term of Cushing's model, absent in the van den Bosch *et al.* model, has the effect of lowering the equilibrium branch from what it would be in the absence of density dependence, and introduces the positive term $-f'(0)/(c\Psi'(0))$. Second, in Cushing's model cannibalism does not increase the adult cannibal's lifespan, and so only immediate recruitment due to cannibalism is counted in the mean yield. Third, the mean yield in Cushing's model does not explicitly depend on juvenile survivorship because survivorship to the juvenile stage is implicit in the conversion factor ζ.

Thus, in the Cushing model, subcritical bifurcation occurs only if the mean yield is greater than one. Moreover, if the mean yield is less than one (and hence the bifurcation is supercritical), then $r/\rho < 1$ and so Cushing's Theorem 7 shows that the introduction of cannibalism for r close to one *decreases* equilibrium levels. Therefore, with respect to the equilibrium levels near $r = 1$ and the direction of bifurcation, cannibalism is beneficial in this model only when the mean yield exceeds one.

Thus, in both the van den Bosch et al. model and the Cushing model, cannibalism is beneficial only when the mean yield exceeds one. Adults can indirectly utilize resources that are available only to juveniles, and this sometimes allows the population to survive when the (adult) resource is too low to maintain the noncannibalistic population.

3. WHEN THE MEAN YIELD IS LESS THAN ONE

In this section, a nonautonomous version of Cushing's cannibalism model is analyzed under the assumptions that (1) juveniles and adults utilize the same resource (so the mean yield is required to be less than one); and (2) the resource level is variable and in fact dips to zero. It will be shown that cannibalism also can be beneficial in this situation.

Consider the following variation on Cushing's (unscaled) discrete adult-on-juvenile cannibalism model:

$$x(t+1) = \left[\beta u(\rho(t))\, e^{-dy(t)} + \gamma c\,\frac{ax(t)}{(a+x(t))}\,\frac{1}{(1+y(t))}\right] y(t) \tag{1}$$

$$y(t+1) = p\left[1 - c\,\frac{a}{(a+x(t))}\,\frac{y(t)}{(1+y(t))}\right] x(t)$$

$$\beta, \gamma, d, a \in (0, \infty); \quad c, p \in [0, 1]$$

$$\gamma < 1.$$

$x(t)$ and $y(t)$ denote the number of juveniles and adults, respectively, at time t, β is the reproductive conversion factor that gives the number of new juveniles per unit resource, $\rho(t)$ is the level of resource at time t, and $u\colon [0, \infty) \to [0, \infty)$ is the per capita adult resource uptake per unit time and satisfies

$$u(0) = 0 \quad \text{and} \quad u'(\rho) > 0 \quad \text{for all} \quad \rho > 0.$$

The reproductive conversion factor γ gives the number of new juveniles per cannibalization, and p represents the probability that a juvenile will mature in the absence of cannibalism.

$$c\,\frac{a}{a+x(t)}\cdot\frac{y(t)}{1+y(t)}$$

is the probability that a juvenile will be cannibalized, and c is the "cannibalism coefficient" which indicates the strength of the cannibalism interaction.

In general one would expect p to be an increasing function of ρ and c to be a decreasing function of ρ; for simplicity p and c are assumed constant. As in Cushing's model, the unit of noncannibalistic resource is defined so that it supplies the same energy as one cannibalized juvenile; hence

$$\beta = \gamma.$$

Since we are assuming juveniles and the adults utilize exactly the same resource in the cannibalism model (1),

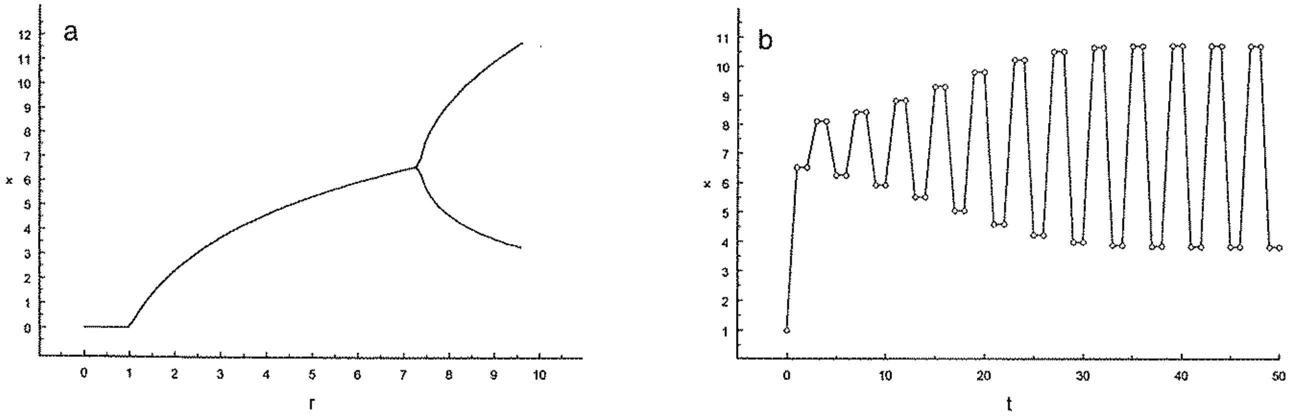

FIG. 1. a. The juvenile component of the attractor as a function of net reproductive number r. A branch of positive equilibria bifurcates supercritically from zero at $r = 1$. The branch loses stability at $r = e^2$ when the eigenvalues pass through $\pm i$, and bifurcates into a 4-cycle (see Fig. 1b). In this simulation $a = 1$, $c = 0$, $\beta = 0.8$, $d = 0.3$, $p = 1$. b. Juveniles as a function of time. The attractor is a 4-cycle with range of cardinality two. In this time series $r = 8.8$, $a = 1$, $c = 0$, $\beta = 0.8$, $d = 0.3$, $p = 1$.

it is necessary to require that the mean yield be less than one:

$$\beta = \gamma < 1.$$

When $c = 0$, the cannibalism model (1) reduces to the noncannibalism model

$$\begin{aligned} x(t+1) &= \beta u(\rho(t))\, e^{-dy(t)} y(t) \\ y(t+1) &= p x(t). \end{aligned} \tag{2}$$

When ρ is constant, Cushing's results show that cannibalism is not beneficial because the mean yield is less than one. His results can be summarized and expanded into the following two remarks [2]. Let $r \doteq \beta u(\rho)\, p$.

Remark 1. When $c = 0$, the trivial (zero) solution of (2) is globally asymptotically stable if $r < 1$ and unstable if $r > 1$. There exists a positive equilibrium $((1/pd) \ln r, (1/d) \ln r)$ of (2) if and only if $r > 1$; this equilibrium is unique when it exists and is locally asymptotically stable when $1 < r < e^2$. (See Fig. 1. See Appendix for proof.)

Remark 2. When $c > 0$, the trivial equilibrium of the cannibalism model (1) is stable if $r < 1$ and unstable if $r > 1$. There is a supercritical bifurcation of positive equilibria at $r = 1$, and a supercritical bifurcation of synchronous 2-cycles at $r = 1$. Near $r = 1$, the positive equilibria are stable if $\beta > 1 - d/c$, in which case the 2-cycles are unstable; and the positive equilibria are unstable if $\beta < 1 - d/c$, in which case the 2-cycles are stable.

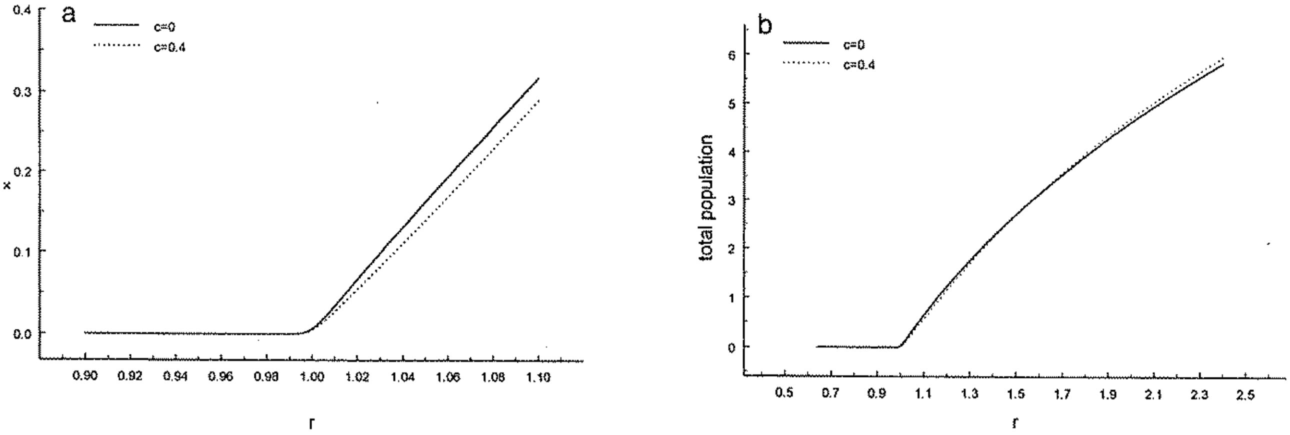

FIG. 2. a. The juvenile component of the attractor as a function of net reproductive number r with $c = 0$ and $c = 0.4$. The introduction of cannibalism lowers the equilibria for $r > 1$ near $r = 1$. In this simulation $a = 1$, $\beta = 0.8$, $d = 0.3$, $p = 1$. b. Total population size attractor as a function of net reproductive number r with $c = 0$ and $c = 0.4$. At larger value of r, the cannibalism can increase equilibrium levels. In this simulation $a = 1$, $\beta = 0.8$, $d = 0.3$, $p = 1$.

Figure 2 compares the bifurcating branches of the noncannibalism model and the cannibalism model. As demonstrated in the Introduction, the advent of cannibalism lowers the equilibrium level at small population sizes (Fig. 2 also suggests, however, that cannibalism may increase equilibria levels at larger population sizes.)

In order to see that cannibalism can be beneficial when the mean yield is *less than* one, consider a simple modification of Cushing's model in which the resource dips to zero for two consecutive time steps. Let ρ be defined as the Heaviside function

$$\rho(t) = MH(t-2) = \begin{cases} 0 & \text{if } 0 \leqslant t \leqslant 1 \\ M & \text{if } t > 1 \end{cases}.$$

It is henceforth assumed that

$$u(\rho) \equiv \rho.$$

In this case all solutions of the noncannibalism model (2) become zero in finite time; the noncannibals cannot survive if the resource vanishes for two consecutive time steps. Positive initial conditions for the cannibalism model (1), however, produce $x(2)$, $y(2) > 0$, and these can be considered the initial conditions for the cannibalism model (1) for $t > 2$ with resource fixed at $\rho = M$.

THEOREM 1. *If $\rho(t) = MH(t-2)$, then*

(1) *all solutions of the noncannibalism model (2) are zero in finite time ($t \geqslant 2$);*

(2) *the trivial solution $(0, 0)$ of the cannibalism model (1) is stable if $r \doteq \beta M p < 1$ and unstable if $r > 1$; and*

(3) *when $r > 1$ the cannibalism model (1) is in fact "uniformly persistent" with respect to the extinction state in the special sense that there exists $\varepsilon > 0$ such that for all $x(0)$, $y(0) > 0$, $\liminf_{t \to \infty} \|(x(t), y(t))\| > \varepsilon$.*

Proof. Let $\rho(t) = MH(t-2)$ in the cannibalism model (1). Note that $x(1)$, $y(1)$, $x(2)$, and $y(2)$ can be made arbitrarily small provided $x(0)$ and $y(0)$ are chosen sufficiently chose to zero, and that $x(2) = y(2) = 0$ if and only if $x(0) = 0$ or $y(0) = 0$.

Let $r \doteq \beta M p < 1$ and $\varepsilon > 0$. Since $(0, 0)$ is stable for the model with $\rho(t) \equiv M$, there exists a δ with $0 < \delta \leqslant \varepsilon$ such that whenever $\|(x(2), y(2))\| < \delta$, we have $\|(x(t), y(t))\| < \varepsilon$ for all $t \geqslant 2$. Also, there exists $\gamma > 0$ such that $\|(x(t), y(t))\| < \delta \leqslant \varepsilon$ for $t = 1, 2$ whenever $\|(x(0), y(0))\| < \gamma$. Thus, the trivial solution is stable when $r < 1$.

Let $r > 1$. The eigenvalues of the linearization at $(0, 0)$ of the model with $\rho(t) \equiv M$ are $\pm\sqrt{r}$, and so $(0, 0)$ is a repellor for $t \geqslant 2$ by the Stable Manifold Theorem for maps [12]. Thus for some $\varepsilon > 0$, for all $(x(2), y(2)) \neq (0, 0)$, there exists $T > 2$ satisfying $\|(x(t), y(t))\| > \varepsilon$ for all $t \geqslant T$. Since $(x(2), y(2)) \neq (0, 0)$ whenever $x(0) > 0$ and $y(0) > 0$, $(0, 0)$ is unstable, and in fact for all $x(0)$, $y(0) > 0$, $\liminf_{t \to \infty} \|(x(t), y(t))\| > \varepsilon$. ∎

This simple nonautonomous modification of Cushing's model definitively shows that, *even when the mean yield is less than one, cannibals may be able to survive times of low resource while noncannibals cannot.* In the next section, an example is presented in which the resource is allowed to fluctuate periodically.

4. EXAMPLE

In Section 3 it was shown that a cannibalistic population (even one whose mean yield is less than one) can survive a single catastrophic drop in resource abundance that would wipe out a noncannibalistic population. In this section it is suggested, by means of an numerical study, that such a cannibalistic population can in fact survive indefinitely in the face of repeated, periodically occurring, resource abundance drops.

Consider model (1) with a P-periodically forced resource defined by the first period

$$\rho(t) = \begin{cases} 0 & \text{if } 0 \leqslant t \leqslant 1 \\ M & \text{if } 1 < t \leqslant P-1 \end{cases}$$

where amplitude $M > 0$ and period $P \in \{3, 4, \ldots\}$. It seems reasonable that the cannibalistic population might survive periodic resource dips provided the recovery times are sufficiently rich in resource and sufficiently long, i.e., provided M and P are sufficiently large. Given a fixed finite period P, one would in general expect a branch of positive P-periodic solutions of the cannibalism model (1) to bifurcate from zero at a critical value of M, with a typical exchange of stability between the trivial solution and the bifurcating branch [14]. The existence and stability of such solutions would imply the possible persistence of the cannibalistic population in a P-periodic state. However, bifurcation theory does not apply at $x = y = 0$ since the linearization of the Pth composite map has two zero eigenvalues; indeed, the trivial solution never loses local stability.

In order to look numerically for P-periodic solutions of the cannibalism model (1), one can fix P and vary M as a bifurcation parameter. Figure 3 shows simulations in which $P = 4$. Stable 4-periodic solutions of (1) exist for large enough cannibalism coefficient c and sufficiently large values of M. Figure 4 shows the trade-off between M and P with $P = 5$ and $P = 6$. The larger the period P,

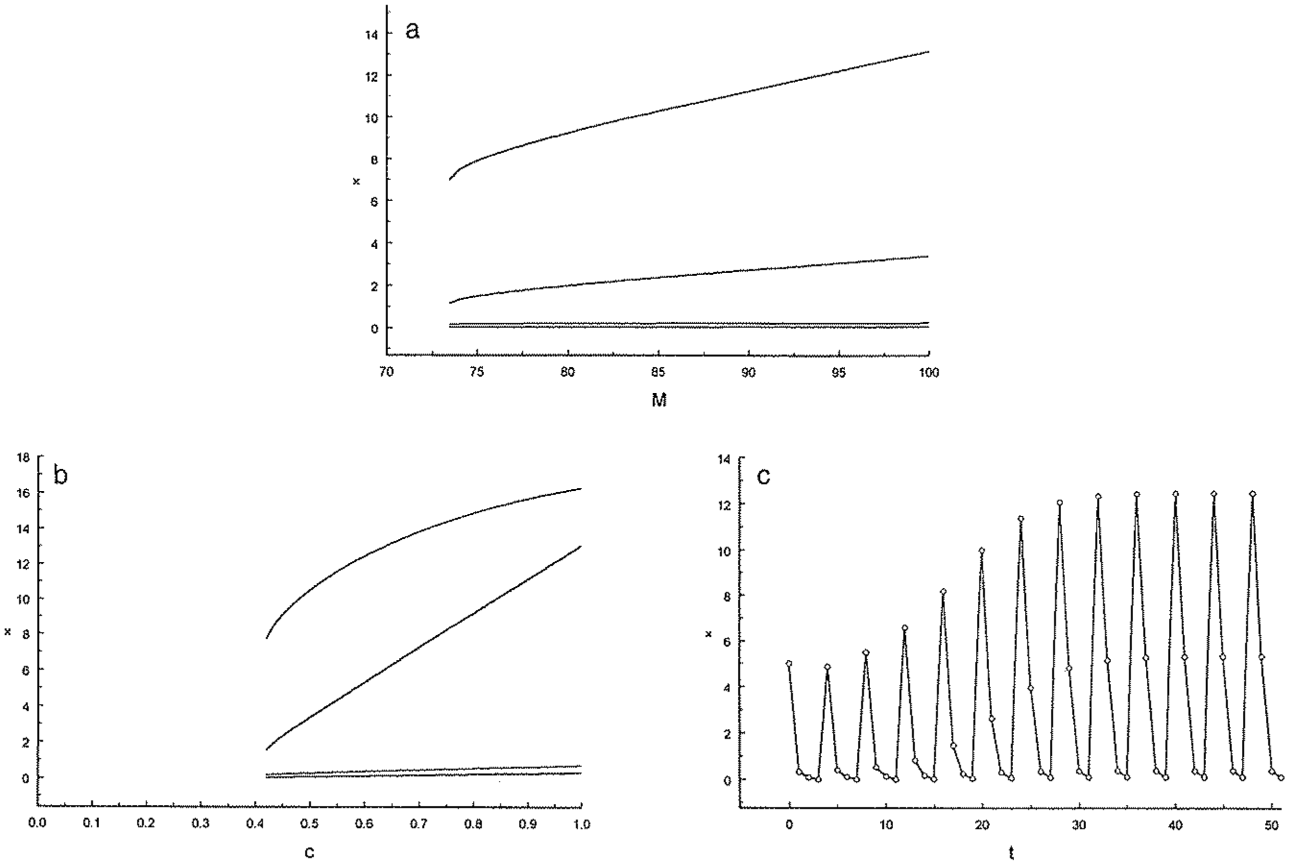

FIG. 3. a. The juvenile component of the attractor as a function of M when $P=4$. Locally stable 4-cycle solutions exist for sufficiently large M but the zero solution is always locally stable. In this simulation $a=1$, $c=0.4$, $\beta=0.8$, $d=0.3$, $p=1$, $P=4$. b. The juvenile component of the attractor as a function of c when $P=4$ and $M=70$. Locally stable 4-cycle solutions (see Fig. 3c) exist for sufficiently large c but the zero solution is always locally stable. In this simulation $a=1$, $\beta=0.8$, $d=0.3$, $p=1$, $P=4$, $M=70$. c. Juveniles as a function of time. The attractor is a 4-cycle. In this time series $a=1$, $c=0.6$, $\beta=0.8$, $d=0.3$, $p=1$, $P=4$, $M=70$.

the smaller M need be in order to allow survival of the population.

In general an analytical investigation seems difficult since (1) linearization of the composite map about zero yields the zero matrix, rendering standard bifurcation theory inapplicable; and (2) computation of the equilibrium equations for the composite maps and their roots appears intractable. Therefore, we will consider one case in detail in order to illustrate numerically the possibility of the persistence of the cannibalistic population.

The case $M=70$ and $P=4$ is investigated numerically as a representative case of large M. Since the zero solution of the cannibalism model (1) is always stable, the 4-cycles seen in Fig. 3b cannot bifurcate from zero. In order to "unfold" a larger picture of these dynamics, consider the 4-periodic resource defined, over the first period, by

$$\rho(t)=\begin{cases} m & \text{if } 0\leqslant t\leqslant 1 \\ M & \text{if } 1<t\leqslant 3 \end{cases}$$

where $0\leqslant m<M$. We now consider the attractor in c-m-x space with $M=70$ and $P=4$.

Figure 5 shows the equilibria of the 4th composite map in c-m-x space; this is one of the range values of the 4-cycle attractor for the cannibalism model (1) and is used for graphical convenience. In the $c=0$ plane, a positive branch of 4-cycles bifurcates supercritically with respect to m at a critical value $m_{cr}\cong 0.2$. As c is increased, the branch develops a kink in which it bends back to the left, then back to the right. Further increases in c cause the leftmost bend to advance further to the left, until for $c\cong 0.45$ it finally crosses through the $m=0$ plane. The upper part of the bend is stable; *hence stable 4-cycles exist at* $m=0$ *for sufficiently large* c. Note that the stable 4-cycles also exist (for sufficiently large c) at small values of $m<m_{cr}$ for which the noncannibals cannot survive.

Thus, when m *is less than a positive critical value* m_{cr}, *the noncannibals cannot survive, while the cannibals may survive for some values of M, P, and c. In particular, in the*

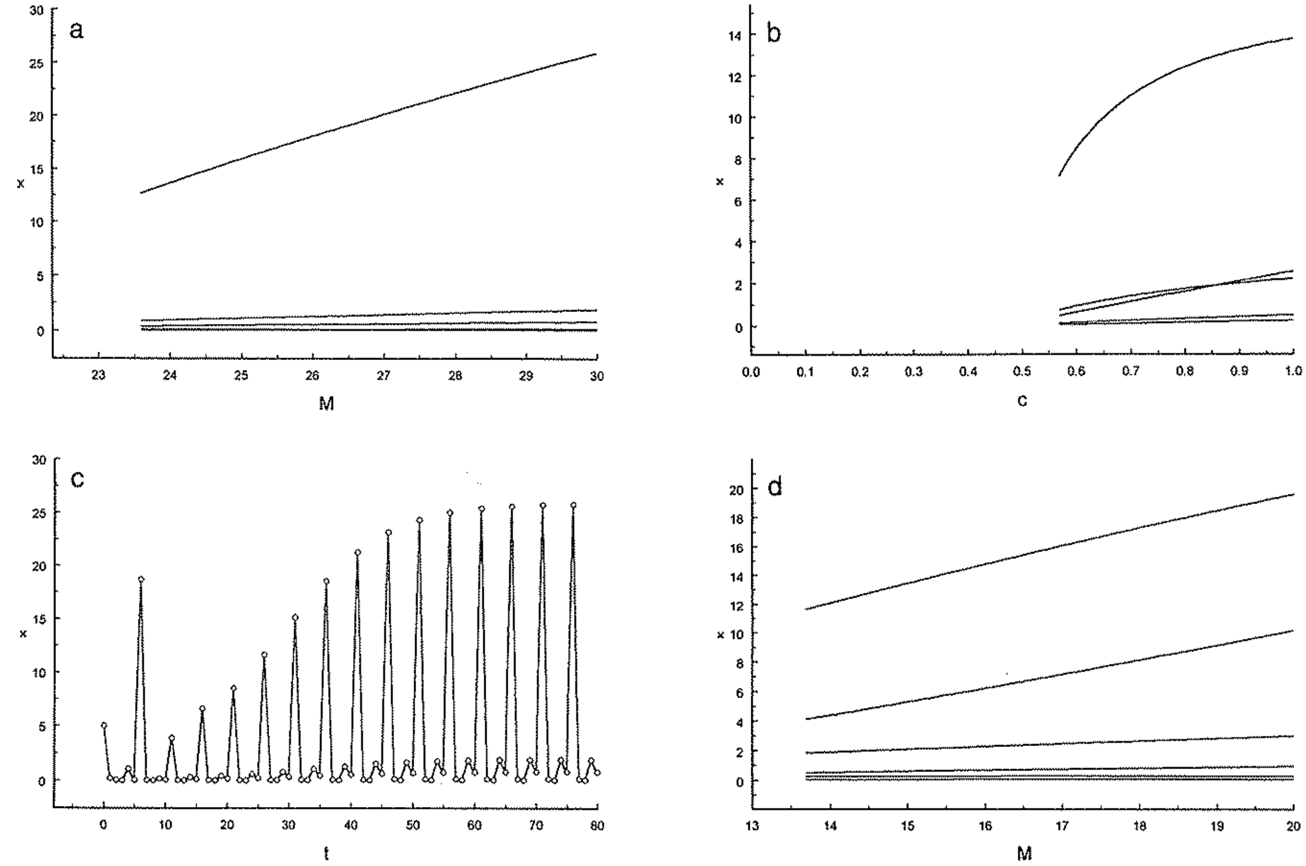

FIG. 4. a. The juvenile component of the attractor as a function of M when $P = 5$. Locally stable 5-cycle solutions exist for sufficiently large M but the zero solution is always locally stable. In this simulation $a = 1$, $c = 0.4$, $\beta = 0.8$, $d = 0.3$, $p = 1$, $P = 5$. b. The juvenile component of the attractor as a function of c when $P = 5$. Locally stable 5-cycle solutions (see Fig. 4c) exist for sufficiently large c but the zero solution is always locally stable. In this simulation $a = 1$, $\beta = 0.8$, $d = 0.3$, $p = 1$, $P = 5$, $M = 15$. c. Juveniles as a function of time. The attractor is a 5-cycle. In this time series $a = 1$, $c = 0.4$, $\beta = 0.8$, $d = 0.3$, $p = 1$, $P = 5$, $M = 30$. d. The juvenile component of the attractor as a function of M when $P = 6$. Locally stable 6-cycle solutions exist for sufficiently large M but the zero solution is always locally stable. In this simulation $a = 1$, $c = 0.4$, $\beta = 0.8$, $d = 0.3$, $p = 1$, $P = 6$.

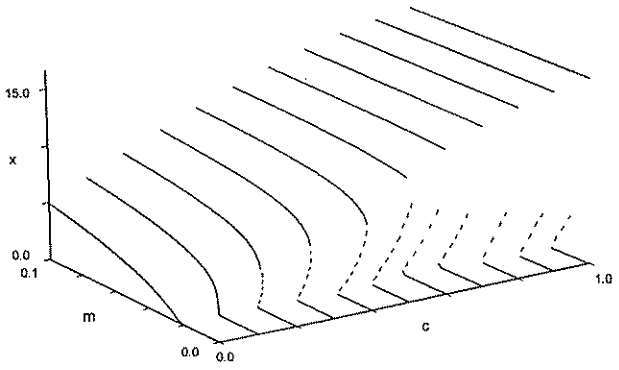

FIG. 5. The juvenile component of the attractor of the 4th composite map as a function of c and m when $P = 4$ and $M = 70$. This is one of the branches of the 4-cycle solution. See text for description. In this simulation $a = 1$, $\beta = 0.8$, $d = 0.3$, $p = 1$, $P = 4$, $M = 70$.

most catastrophic case $m = 0$, the noncannibal population goes extinct in finite time, while the cannibal population can survive.

Further simulations for different parameter values and for different values of P and M have exhibited similar results and conclusions.

5. CONCLUSION

The van den Bosch *et al.* concept of mean yield is a key factor in the dynamics of cannibalistic populations. When the cannibalized individuals have access to a resource which is not available to the cannibals, the mean yield can exceed one at low (adult) resource levels. When there is no differentiation between the resource of the cannibals and the cannibalized individuals, however, the mean yield is less than one at low resource levels. In the van den Bosch *et al.* and Cushing models, cannibalism is beneficial only when the mean yield exceeds one. In this paper it has been shown that under certain circumstances cannibalism can be beneficial even when the mean yield is less than one.

Specifically, a variation (1) of Cushing's model was analyzed under the assumptions that (1) the mean yield is less than one; and (2) the resource dips to zero for two consecutive time intervals:

$$\rho(t) = \begin{cases} 0 & \text{if } 0 \leqslant t \leqslant 1 \\ M & \text{if } t > 1 \end{cases}$$

In this case the noncannibal population goes extinct in finite time while the cannibal population is uniformly persistent.

When the resource fluctuates P-periodically with

$$\rho(t) = \begin{cases} m & \text{if } 0 \leqslant t \leqslant 1 \\ M & \text{if } 1 < t \leqslant P-1 \end{cases}$$

$0 \leqslant m < M$, simulations suggest that there exist stable, positive P-periodic solutions to the cannibalism model (1) if M is sufficiently large, and, if m is also large enough, to the cannibalism model (2) as well. However, when m is less than some positive critical value m_{cr}, the noncannibals cannot survive, while the cannibals may survive for some values of M, P, and c. In particular, if $m = 0$, the noncannibal population goes extinct in finite time, while the cannibal population can survive.

A number of points can be made about the case $m = 0$. First, there is an inverse relationship between the period P and the maximal resource level M. The smaller the level M of high resource, the longer the duration of high resource must be in order to allow the cannibal population to exist. Second, P-periodic resource fluctuations give rise to P-periodic solutions of the cannibalism model. Third, the cannibal population can survive only if the population size is sufficiently large (since the trivial solution is always locally stable), if the cannibalism coefficient c is sufficiently large, and if the mean yield is not too small. Fourth, catastrophic collapse may occur if c is too small, or if the initial population size is too small.

6. APPENDIX

Proof of Remark 1. The linearization at zero of (2) has eigenvalues

$$\lambda = \pm\sqrt{r},$$

and hence the trivial solution is stable when $r < 1$ and unstable when $r > 1$.

Let $r < 1$. Since

$$x(t+2) = re^{-dp\,x(t)}x(t) < x(t)$$
$$y(t+2) = re^{-dy(t)}y(t) < y(t),$$

the sequences $\{x(2k)\}_{k=0}^{\infty}$ and $\{y(2k)\}_{k=0}^{\infty}$ are decreasing and hence approach nonnegative limits X and Y. If either of X or Y were positive, then one of the equations

$$1 = re^{-dpX}$$
$$1 = re^{-dY}$$

would hold, which is impossible. Thus, $X = Y = 0$. The same argument holds for the sequences $\{x(2k+1)\}_{k=0}^{\infty}$ and $\{y(2k+1)\}_{k=0}^{\infty}$, and so the trivial solution is globally stable.

The equilibria equations for $x, y \neq 0$ are equivalent to

$$1 = re^{-dy}$$
$$y = px$$

from which follow the existence and uniqueness of the positive equilibrium for $r > 1$. The linearization of (2) at the positive equilibrium has eigenvalues

$$\lambda = \pm\sqrt{1 - \ln r},$$

and hence the equilibrium is locally asymptotically stable when $1 < r < e^2$. ∎

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REFERENCES

[1] Cushing, J. M. 1985. Equilibria in structured populations, *J. Math. Biol.* **23**, 15–39.

[2] Cushing, J. M. 1991. A simple model of cannibalism, *Math. Biosci.* **107**, 47–71.

[3] Cushing, J. M. 1992. A size-structured model for cannibalism, *Theor. Pop. Biol.* **42**, 347–361.

[4] Cushing, J. M., and Li, J. 1995. Oscillations caused by cannibalism in a size-structured population model, *Can. J. Appl. Math.* **3**, No. 2.

[5] Diekmann, O., Nisbet, R. M., Gurney, W. S. C., and van den Bosch, F. 1986. Simple mathematical models for cannibalism: a critique and a new approach, *Math. Biosci.* **78**, 21–46.

[6] Elgar, M. A., and Crespi, B. J. Eds. 1992. "Cannibalism: Ecology and Evolution Among Diverse Taxa," Oxford Univ. Press, Oxford.

[7] Elgar, M. A., and Crespi, B. J. 1992. Ecology and evolution of cannibalism, *in* "Cannibalism: Ecology and Evolution Among Diverse Taxa" (M. A. Elgar and B. J. Crespi, Eds.), pp. 1–12, Oxford Univ. Press, Oxford.

[8] Fox, L. R. 1975. Cannibalism in natural populations, *Ann. Rev. Ecol. Syst.* **6**, 87–106.

[9] Gabriel, W. 1985. Can cannibalism be advantageous in cyclopoids? A mathematical model, *Verh. Internat. Verein. Limnol.* **22**, 3164–3168.

[10] Gabriel, W. 1985. Overcoming food limitations by cannibalism: A model study on cyclopoids, *Arch. Hydrobiol. Beih.* **21**, 373–381.

[11] Gabriel, W. 1985. Simulation komplexer Populationsdynamik, *in* "Simulationstechnik" (D. P. F. Moller, Ed.), pp. 318–324, Vol. 109, Informatik Fachberichte.

[12] Guckenheimer, J., and Holmes, P. 1983. "Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields," Springer-Verlag, New York, p. 18.

[13] Gurtin, M. E., and Levine, D. S. 1982. On populations that cannibalize their young, *SIAM J. Appl. Math.* **42**, 94–108.

[14] Henson, S. M. 1996. Existence and stability of nontrivial periodic solutions of periodically forced discrete dynamical systems, *J. Differ. Equations Appl.* **2**, 315–331.

[15] Hofbauer, J., and So, J. W.-H. 1989. Uniform persistence and repellors for maps, *Proc. Amer. Math. Soc.* **107**, 1137–1142.

[16] Landhahl, H. D., and Hansen, B. D. 1975. A three stage population model with cannibalism, *Bull. Math. Biol.* **37**, 11–17.

[17] Polis, G. A. 1981. The evolution and dynamics of intraspecific predation, *Ann. Rev. Ecol. Syst.* **12**, 225–251.

[18] van den Bosch, F., de Roos, A. M., and Gabriel, W. 1988. Cannibalism as a lifeboat mechanism, *J. Math. Biol.* **26**, 619–633.

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