

ON THE STABILIZING EFFECT OF CANNIBALISM IN STAGE-STRUCTURED POPULATION MODELS

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ABSTRACT. In this paper we give a contribution to the systematic investigation of cannibalism in predator-prey models commenced since the publication of the paper by Kohlmeier and Ebenhöh in 1995. We present a stage-structured predator-prey model and study its dynamics. We use a Hopf bifurcation analysis to prove that cycles are possible and that cannibalism suppresses these cycles; that is, when cannibalism attack rate is increased so that it passes a critical value, the coexistence steady state changes from being unstable to being stable. Numerical simulations are provided together with the mathematical analysis. Our modelling approach is based on balance arguments and a comparison with some early models which predict that a destabilizing effect of cannibalism is performed. Our results agree with the output of growth simulation for some cannibalistic copepods.

1. Introduction. Adults preying on juveniles of the same species have been widely documented in nature [10]. For example, this behaviour has been observed for a variety of fish species, such as Atlantic cod [1], salmon, perch and striped bass (see [12] and the reference contained therein) as well as copepods [24].

This phenomenon has been the subject of a wide mathematical literature, and numerous modelling approaches have been proposed. For example, the McKendrick-von Foerster model for age-structured populations has been implemented for studies on cannibalism by M. E. Gurtin and his coauthors (see, e.g., [12]). Their model is still inspiring a series of papers (see, e.g., [20]). A further example stands in discrete stage-structured models. For such models one can refer to the papers by J. M. Cushing and his coauthors (see, e.g., [5] and the reference contained therein). This approach has been recently applied to study cannibalism in Atlantic cod [27]. For a deeper survey on the population dynamic theory of cannibalism and the related literature, we refer to the recent review [4].

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In the present paper we are concerned with a specific class of models, i.e., predator-prey models where the predator is stage structured and has an instantaneous maturation rate. The analysis focuses mainly on the stabilizing-destabilizing effect of cannibalism.

Our study is motivated by the following discussion. In 1995 Kohlmeier and Ebenhöf [15] showed that cannibalism could stabilize a predator-prey system. A high cannibalism rate may cause the internal steady state to change from being unstable to stable. The same conclusion has been pointed out by van den Bosch and Gabriel [22] for an age-structured predator-prey system. This conclusion has been regarded as somewhat surprising (see, e.g., [14]) because of several disadvantages that cannibalism presents for populations that practise it. For example, the cannibalism would waste the high-cost energy needed for breeding (see, e.g., [18]). In 1999 K.G. Magnusson [16] and, more recently, Kaewmanee and Tang [14] presented a predator-prey continuous model including cannibalism, which shows that cannibalism has a destabilizing effect. In [14] the result obtained by Kohlmeier and Ebenhöf is explained as a consequence of the use of a Holling type-II functional response. This implies that a predatory switching is included in the model, which would have a stabilizing effect. On the other hand, the predator-prey cycles in [22] are viewed as essentially generated by the age structure. Increasing the cannibalism attack rate would diminish the effects of the age structure.

In this paper we give a new possible approach to predator-prey interaction including predators' cannibalism and study the effect of cannibalism on the related model. The model and the results are compared with the ones presented in [14] and [16].

The paper is organized as follows. In section 2 the models quoted in this introduction are recalled in some detail, and some relevant aspects are discussed. In section 3 our model is presented. Its analysis is performed in section 4, where the main result of the paper is stated. In section 5 numerical simulations complete the discussion. The conclusions contained in section 6 close the paper.

2. Predator-prey models including cannibalism: survey and shortcomings. In 1995 Kohlmeier and Ebenhöf [15] published the first of a series of systematic investigations on predator-prey systems with cannibalistic predators. They considered a predator-prey system with logistic prey growth. The Holling type-II functional response was used to describe the predator uptake. The model they considered is the following:

$$\begin{aligned} \frac{dz}{dt} &= rz \left(1 - \frac{z}{K}\right) - \alpha f(z, x)x \\ \frac{dx}{dt} &= \gamma \alpha f(z, x)x - \omega x - \theta g(z, x)x, \end{aligned} \quad (1)$$

where

$$f(z, x) = \frac{z}{1 + \alpha h_1 z + \theta h_2 x}; \quad g(z, x) = \frac{x}{1 + \alpha h_1 z + \theta h_2 x}.$$

In (1), $z(t)$ and $x(t)$ are the density of prey and predator, respectively; r and K are the growth rate and carrying capacity of the prey population; α and θ are the attack rates on prey and conspecifics; h_1 and h_2 are the handling times of prey and conspecifics; γ is the predator yield, that is, the conversion efficiency of eaten prey into predator biomass, and ω is the predator death rate.

The analysis of this model allowed the authors to conclude that cannibalism is a stabilizing mechanism, in the sense that when the cannibalism attack rate θ increases, the internal steady state changes from unstable to stable.

Van den Bosch and Gabriel [22] have emphasized that oscillations in model (1) are due to the interaction of logistic prey growth and the hyperbolic functional response. They asked themselves if oscillations could also be due to other mechanisms. Precisely, they proposed an age-structured model and showed that cannibalism is a stabilizing mechanism also when population oscillations are due to this age structure. They concluded that in predator-prey systems, cannibalism by predators can stabilize both externally generated (consumer-resource) as well as internally generated (age-structure) fluctuations. The model they considered is a structured model where the predators may have four stages: small juveniles S , vulnerable juveniles V , large juveniles L and adults A . The juvenile stage has fixed duration time \bar{a} and juveniles are vulnerable to cannibalism only in the fixed interval $[a_1, a_2]$. Prey z is not divided into classes. Their model reads as follows:

$$\begin{aligned} \frac{dz}{dt} &= rz \left(1 - \frac{z}{K}\right) - \alpha z A \\ \frac{dS}{dt} &= \xi \alpha z A - \varphi_S(z, A) - \mu S \\ \frac{dV}{dt} &= \varphi_S(z, A) - \varphi_V(z, A) - \mu V - \theta AV \\ \frac{dL}{dt} &= \varphi_V(z, A) - \varphi_L(z, A) - \mu L \\ \frac{dA}{dt} &= \varphi_L(z, A) - \omega A. \end{aligned} \quad (2)$$

In (2) the parameter μ represents the juvenile death rate. The other parameters have the same meaning as in model (1). The functions φ represent the maturation rates from one stage to the next one. For example, the rate at which individuals age from S into the vulnerable class V equals the rate of birth at time $t - a_1$ multiplied by the probability that an individual born at $t - a_1$ is still alive at time t . When the maturation from V to L is formulated, the probability to survive to cannibalism is also considered. This probability is found from the first term of Poisson distribution. These considerations lead to the following form for the functions φ :

$$\begin{aligned} \varphi_S(z, A) &= \xi \alpha z(t - a_1) A(t - a_1) \exp(-\mu a_1) \\ \varphi_V(z, A) &= \xi \alpha z(t - a_2) A(t - a_2) \exp\left(-\mu a_2 - \theta \int_{t-(a_2-a_1)}^t A(\sigma) d\sigma\right) \\ \varphi_L(z, A) &= \xi \alpha z(t - \bar{a}) A(t - \bar{a}) \exp\left(-\mu \bar{a} - \theta \int_{t-(\bar{a}-a_1)}^{t-(\bar{a}-a_2)} A(\sigma) d\sigma\right). \end{aligned}$$

In 1999 Magnusson [16] reconsidered the use of predator-prey models for the analysis of cannibalism's role (and in particular its stabilizing or destabilizing effect). He stressed that in model (1) the absence of structure means that the predator feeds on itself. On the other hand, he remarked that in model (2) the only effect of cannibalism is additional mortality for the vulnerable class of juveniles (the last term in the third equation of system (2)), so that the consumption of juveniles does not influence the growth rates of adults.

The model proposed by Magnusson is a system with three ordinary differential equations. He assumed an instantaneous maturation into the adult class, instead of a delayed one as in (2), and a constant per capita rate of maturation k_M . He also stressed that the simplifying assumption of instantaneous maturation means that the oscillations that may occur are not caused by a delay inherent in the system,

as in (2). The model he proposed reads

$$\begin{aligned} \frac{dz}{dt} &= rz \left(1 - \frac{z}{K}\right) - \alpha z A \\ \frac{dJ}{dt} &= \beta A - k_M J - sAJ - k_J J \\ \frac{dA}{dt} &= k_M J + \gamma sAJ + k_z Az - k_A A, \end{aligned} \quad (3)$$

where z , A and J are the measure (biomasses) of prey, adult predators and juvenile predators, respectively. The parameter γ is the conversion efficiency of eaten juveniles into adult biomass. He found that if the mortality rate of juveniles is high and/or the recruitment rate of mature population is low, then there exists a unique internal equilibrium which is stable for low levels of cannibalism, but a loss of stability by a Hopf bifurcation will take place as the level of cannibalism increases. He concluded therefore that cannibalism can have a destabilizing effect in a predator-prey system.

In 2003 Kaewmanee and Tang [14] reexamined model (3). By means of a different rescaling they obtained the same results as in [16]; i.e., the loss of stability by Hopf bifurcation of the internal equilibrium as the level of cannibalism increases. Unlike [16], their results do not require any restriction on the mortality rate of juveniles and on the recruitment rate of mature population.

Model (3) presents an unusual property. It may predict that the predator can persist in the absence of the prey; that is an equilibrium of kind $E_{z_0} \equiv (0, J^*, A^*)$ exists which may be stable in the AJ -plane. Magnusson notes that the existence of such a state means that the predator is only partially coupled to the prey. In other words, the predator has an alternative food source, which is not modelled explicitly, and the prey species may be *only* the preferred food. Kaewmanee and Tang argue that model (3) does not contain any reference to the second prey population so that it is invisible to the predator species: this means that predators could not feed on them when the primary prey species becomes extinct. They conclude that the above steady state E_{z_0} would be impossible. Nevertheless, this equilibrium is still admissible for their model.

In (3) the variables are expressed in terms of biomasses. The interactions consist in source uptake and consequent growth through suitable yields. The predator birth rate is independently defined as a linear function of adult predators. The circumstance that the model (3) may predict that the predator sustains itself at a steady state with no recourse to the prey, comes essentially from the assumption of a constant birth rate. This can be verified by observing that the dynamics of perturbations with initially zero z -component is ruled by

$$\begin{aligned} \frac{dJ}{dt} &= \beta A - k_M J - sAJ - k_J J \\ \frac{dA}{dt} &= k_M J + \gamma sAJ - k_A A. \end{aligned}$$

It is easy to verify that the origin is unstable if $k_M \beta > k_A(k_M + k_J)$. Further, if

$$k_A \gamma^{-1} < \beta < k_A k_M^{-1} (k_M + k_J),$$

then a positive equilibrium $E = (J^*, A^*)$, where

$$J^* = \frac{k_A(k_M + k_J) - \beta k_M}{s(\gamma - 1)k_M + s\gamma k_J}, \quad A^* = \frac{k_A(k_M + k_J) - \beta k_M}{s(\gamma\beta - k_A)},$$

exists and is stable.

Differently from model (3), our approach expresses the variables in terms of number of individuals, and the adult-prey and adult-juvenile interactions consist of source uptake and conversion (through suitable yields) in new birth. Hence, the

number of adults varies only in cause of mortality and maturation from the juvenile class. This last aspect is common to models in [22], [25] and [26].

3. The model. Assume that $R(t)$ represents the number of individuals of a predator population at time t . Let $R(t) = J(t) + A(t)$, where $A(t)$ and $J(t)$ represent the number of adults and juveniles of the population at time t , respectively. Let $P(t)$ represent the number of individuals of a nonstructured prey population at time t . The classical predator-prey model reads

$$\begin{aligned}\frac{dR}{dt} &= -\alpha R + \beta RP \\ \frac{dP}{dt} &= \gamma_1 P - \gamma_2 P^2 - \delta RP,\end{aligned}$$

where a logistic growth for the prey population in absence of predators has been assumed. Assuming that only the adults may eat the prey, one gets

$$\begin{aligned}\frac{d(A+J)}{dt} &= -\alpha(A+J) + \eta_I \delta AP \\ \frac{dP}{dt} &= \gamma_1 P - \gamma_2 P^2 - \delta AP,\end{aligned}$$

where η_I is the yield; i.e., it denotes the coefficient in converting prey into new immature predators (juveniles). Now we separate the dynamics of A and J , taking into account that A and J have different death rates, d_A and d_J , and assuming that the juveniles mature at a constant rate M . One has

$$\begin{aligned}\frac{dA}{dt} &= MJ - d_A A \\ \frac{dJ}{dt} &= \eta_I \delta AP - MJ - d_J J \\ \frac{dP}{dt} &= \gamma_1 P - \gamma_2 P^2 - \delta AP.\end{aligned}\tag{4}$$

The cannibalism is assumed to have the same mechanism of prey uptake: some amount σAJ is taken from J by A and a new amount $\eta_C \sigma AJ$ contributes to the juvenile birth rate, where η_C denotes the coefficient in converting juveniles into new juveniles. This choice means that a balance between killing (i.e., victim mortality) and energy extraction (according to the terminology used by Claessen and his coworkers; see [4]) has been included in the evolution equation of juveniles. Model (4) with the inclusion of the cannibalism reads

$$\begin{aligned}\frac{dA}{dt} &= MJ - d_A A \\ \frac{dJ}{dt} &= \eta_I \delta AP - (1 - \eta_C) \sigma AJ - MJ - d_J J \\ \frac{dP}{dt} &= \gamma_1 P - \gamma_2 P^2 - \delta AP.\end{aligned}\tag{5}$$

Set now the following nondimensional variables and parameters as follows:

$$x = \frac{\delta}{d_A} A; \quad y = \frac{M\delta}{d_A^2} J; \quad z = \frac{\gamma_2}{d_A} P; \quad \tau = d_A t;$$

$$a = \eta_I M \delta / \gamma_2 d_A; \quad b = \sigma / \delta; \quad c = (M + d_J) / d_A; \quad d = \gamma_1 / d_A.$$

System (5) becomes

$$\begin{aligned}\frac{dx}{d\tau} &= y - x \\ \frac{dy}{d\tau} &= axz - b(1 - \eta_C)xy - cy \\ \frac{dz}{d\tau} &= dz - z^2 - xz.\end{aligned}\tag{6}$$

Throughout the paper, we will assume that $\eta_C < 1$. This assumption means that the killing always prevails over the energy extraction. This does not allow the model to represent some aspect of cannibalism which derives from a prevailing energy gain, as for example the so-called ‘‘life-boat mechanism,’’ which enables a cannibalistic population to survive periods of food shortage, whereas a non-cannibalistic

but otherwise identical population would go extinct. A way to overcome this simplification should be to consider a more complex nonlinearity through a suitable functional response. For example, the cannibalistic term in the second equation of system (6) might give a positive contribution to juvenile growth when the presence of prey is scarce. However, there is no biological evidence (as far as we know) for the possible correct form of such functional response and for the parameters to be included therein. Hence, we here limit ourselves to consider a bilinear term as a local approximation of a more complex (and biologically more unsure) nonlinearity. From a mathematical point of view, this assumption avoids the existence of an equilibrium at $(x^*, y^*, 0)$.

4. Model analysis.

4.1. Absorbing set. We start our analysis by proving the existence of an absorbing set for system (6). First, it can be easily seen that the set

$$\{(x, y, z) : x > 0, y > 0, z \geq 0\}$$

is positively invariant for the solution to system (6). Further, from the third equation of system (6) it follows that a positive constant M exists such that $z(t) < M$ for large t . Now set

$$X = \alpha x; \quad \text{and} \quad Y = \beta y + \gamma,$$

where α , β and γ are positive constants to be chosen later. On the solutions to (6) it follows that:

$$\begin{aligned} \frac{1}{2} \frac{d}{d\tau} (X^2 + Y^2) &= \alpha^2 x \dot{x} + \beta (\beta y + \gamma) \dot{y} \\ &\leq \alpha^2 xy - X^2 + Y [a\beta Mx - b\beta(1 - \eta_c)xy - cY + c\gamma] \\ &= -X^2 - cY^2 + c\gamma Y + \alpha^2 xy + a\beta^2 Mxy - b\beta^2(1 - \eta_c)xy^2 + a\beta M\gamma x - b\beta\gamma(1 - \eta_c)xy \end{aligned}$$

Now let be α , β and γ such that:

$$\alpha^2 + a\beta^2 M = b\beta\gamma(1 - \eta_c).$$

It follows that

$$\frac{1}{2} \frac{d}{d\tau} (X^2 + Y^2) \leq -X^2 - cY^2 + c\gamma Y + a\beta M\gamma x.$$

But given the Cauchy inequality,

$$c\gamma Y \leq \frac{1}{2} \left(\epsilon_1 c^2 \gamma^2 + \frac{Y^2}{\epsilon_1} \right) \quad \text{and} \quad a\beta M\gamma x \leq \frac{1}{2} \left(\epsilon_2 a^2 M^2 \beta^2 \gamma^2 + \frac{X^2}{\alpha^2 \epsilon_2} \right).$$

Hence,

$$\frac{1}{2} \frac{d}{d\tau} (X^2 + Y^2) \leq - \left[1 - \frac{1}{2\alpha^2 \epsilon_2} \right] X^2 - \left[c - \frac{1}{2\epsilon_1} \right] Y^2 + \frac{1}{2} (\epsilon_1 c^2 \gamma^2 + \epsilon_2 a^2 M^2 \beta^2 \gamma^2).$$

Now choose ϵ_1 and ϵ_2 such that

$$1 - \frac{1}{2\alpha^2 \epsilon_2} = \lambda_1 \quad \text{and} \quad c - \frac{1}{2\epsilon_1} = \lambda_2,$$

where λ_1 and λ_2 are positive constants; set

$$k = \frac{1}{2} (\epsilon_1 c^2 \gamma^2 + \epsilon_2 a^2 M^2 \beta^2 \gamma^2); \quad m = \min(\lambda_1, \lambda_2).$$

It follows that

$$\frac{d}{d\tau} (X^2 + Y^2) + 2m (X^2 + Y^2) \leq 2k.$$

Hence

$$\frac{d}{d\tau} [e^{2m\tau} (X^2 + Y^2)] \leq 2ke^{2m\tau},$$

so that

$$X^2 + Y^2 \leq (X^2(0) + Y^2(0)) e^{-2m\tau} + \frac{k}{m} (1 - e^{-2m\tau}),$$

and hence, setting $u^2 = X^2 + Y^2 + z^2$, it follows that

$$u^2 \leq (X^2(0) + Y^2(0)) e^{-2m\tau} + \frac{k}{m} (1 - e^{-2m\tau}) + M^2, \quad (7)$$

so that u remains bounded as the time tends to infinity:

$$\limsup_{\tau \rightarrow +\infty} |u| \leq \sqrt{km^{-1} + M^2}.$$

Now let us consider the ball $B(0, R_0)$, where $R_0 = \sqrt{km^{-1} + M^2}$. We are in position to prove the following:

PROPOSITION 4.1. *Every ball $B(0, \rho_*)$, where $\rho_* > R_0$, is an absorbing set for system (6).*

Proof. We must show that if C is a bounded set of \mathbf{R}^3 , a time instant τ^* exists such that every solution starting in C belongs to $B(0, \rho_*)$, for $\tau > \tau^*$ [21].

Let $B(0, R)$, where $R > \rho_*$, such that $C \subseteq B(0, R)$, and let us impose that

$$u^2(0) \leq R^2 \Rightarrow u^2(t) \leq \rho_*^2; \quad \text{for all } \tau > \tau^*.$$

It suffices from (7) that

$$u^2 \leq R^2 e^{-2m\tau} + \frac{k}{m} (1 - e^{-2m\tau}) + M^2 < \rho_*^2.$$

Hence

$$\left(R^2 - \frac{k}{m}\right) e^{-2m\tau} < \rho_*^2 - R_0^2.$$

This means that

$$\tau > \tau^* = \frac{1}{2m} \log \frac{R^2 - km^{-1}}{\rho_*^2 - R_0^2} \Rightarrow u^2 < \rho_*^2,$$

which completes the proof. \diamond .

4.2. Equilibria. System (6) admits the trivial equilibria $E_0 \equiv (0, 0, 0)$ and $E_1 \equiv (0, 0, d)$. As for nontrivial equilibria, we observe that a unique equilibrium $E \equiv (x^*, y^*, z^*)$ exists, with

$$x^* = \frac{ad - c}{a + b(1 - \eta_c)}; \quad y^* = x^*; \quad z^* = d - x^*. \quad (8)$$

The inequality

$$0 < \frac{ad - c}{a + b(1 - \eta_c)} < d,$$

that is,

$$ad > c, \quad (9)$$

ensures that E has positive components. It may be observed from (8) that increasing the cannibalistic parameter b results in an increase of the prey steady state z^* and in a decrease of adult x^* and juvenile y^* predator steady states, irrespective of parameter values. This feature accords with the analysis presented in [22] for an age-structured model including delayed juvenile maturation.

The Jacobian matrix corresponding to the generic $\bar{E} = (\bar{x}, \bar{y}, \bar{z})$ reads

$$M(\bar{E}) = \begin{pmatrix} -1 & 1 & 0 \\ a\bar{z} - b(1 - \eta_c)\bar{y} & -b(1 - \eta_c)\bar{x} - c & a\bar{x} \\ -\bar{z} & 0 & d - 2\bar{z} - \bar{x} \end{pmatrix}, \quad (10)$$

so that E_0 is clearly unstable (saddle point). Moreover, where the equilibrium E_1 is concerned,

$$M(E_1) = \begin{pmatrix} -1 & 1 & 0 \\ ad & -c & 0 \\ -d & 0 & -d \end{pmatrix},$$

so that the eigenvalue equation is

$$\lambda^3 + (1 + c + d)\lambda^2 + (c + d + cd - ad)\lambda + (cd - ad^2) = 0.$$

By applying the Routh Hurwitz criterion, one gets eigenvalues that all have negative real parts if

$$1 + c + d > 0$$

$$cd - ad^2 > 0$$

$$(1 + c + d)(c + d + cd - ad) - (cd - ad^2) > 0$$

so that the equilibrium E_1 is unstable if (9) holds, and it is locally stable otherwise. We remark that the stability property of E_0 and E_1 does not depend on the parameter b , which in turn depends on the cannibalism attack rate. This means that the cannibalism per se can not lead to predator extinction.

The local stability of the coexistence equilibrium is pointed out in the following:

PROPOSITION 4.2. *There exists a unique $b^* > 0$ such that E is unstable for $b < b^*$ and locally stable for $b > b^*$.*

Proof. It can be easily seen that, in view of (8), the matrix (10) evaluated for the equilibrium E becomes

$$M(E) = \begin{pmatrix} -1 & 1 & 0 \\ c & -a\varphi & ax^* \\ -\varphi & 0 & -\varphi \end{pmatrix}, \quad (11)$$

where we have set

$$\varphi(b) = \frac{c + bd(1 - \eta_c)}{a + b(1 - \eta_c)}.$$

The eigenvalues are given by

$$\lambda^3 + (1 + \varphi + a\varphi)\lambda^2 + (a\varphi + \varphi + a\varphi^2 - c)\lambda + a\varphi^2 + ax^*\varphi - c\varphi = 0. \quad (12)$$

Searching for roots with negative real parts, an application of the Routh-Hurwitz criterion leads to the following inequality:

$$a(a + 1)\varphi^3 + (3a + a^2 + 1)\varphi^2 + (a + 1 - ac - ad)\varphi - c > 0. \quad (13)$$

When this inequality is satisfied, E is locally stable. If its reverse holds, then E is unstable. Now denote by $\psi(\varphi)$ the left-hand side of (13). We note that $\psi(0) = -c$ and $\psi(+\infty) = +\infty$, so that there exists at least a $\bar{\varphi}$ such that $\psi(\bar{\varphi}) = 0$. Further, consider

$$\psi'(\varphi) = 3a(a + 1)\varphi^2 + 2(3a + a^2 + 1)\varphi + (a + 1 - ac - ad),$$

and set

$$\Delta = (3a + a^2 + 1)^2 - 3a(a + 1)(a + 1 - ac - ad).$$

A straightforward inspection reveals that $\Delta > 0$, so that the equation $\psi'(\varphi) = 0$ admits two negative roots or one positive and one negative root. In the first case $\psi'(\varphi) > 0$, for all $\varphi > 0$. Hence there exists a unique $\bar{\varphi} > 0$ such that

$$\psi(\bar{\varphi}) = 0; \quad \psi(\varphi) < 0 \text{ for } 0 < \varphi < \bar{\varphi} \text{ and } \psi(\varphi) > 0 \text{ for } \varphi > \bar{\varphi}. \quad (14)$$

In the second case the function $\psi(\varphi)$ has a negative minimum for some φ_m and (14) holds for a unique $\bar{\varphi} > \varphi_m$.

In view of the monotonicity of the function $\varphi(b)$ we obtain that there exists a unique

$$b^* = \frac{a\bar{\varphi} - c}{(1 - \eta_c)(d - \bar{\varphi})} \quad (15)$$

such that the inequality (13) holds for $b > b^*$ and its reverse holds for $b < b^*$. The proposition is hence proved. \diamond

REMARK 1. *To ensure the positiveness of b^* , the condition $\bar{\varphi} > c/a$ should be imposed. On the other hand it is easy to verify that its reverse, $\bar{\varphi} < c/a$, implies $ad < c$ so that in this case the equilibrium E is not in the positive orthant.*

Proposition 4.2 ensures the local stability of E for $b > b^*$. We stress that the global analysis might be performed with the geometrical approach based on the use of a higher-order generalization of the Bendixson's criterion which has applied in [2] and [3] for a system with a structure very similar to (6). However, we leave this investigation to later studies, and here instead we focus on the analysis of Hopf bifurcation, which may give answers on possible oscillations when the cannibalism attack rate is varied.

4.3. Hopf bifurcation. We state the following:

PROPOSITION 4.3. *The threshold $b = b^*$, where b^* is given by (15), is a Hopf bifurcation point.*

Proof. According to the Hopf Theorem [11], at the Hopf bifurcation point the characteristic polynomial of (11) must have a pair of purely imaginary roots, say $\pm i\beta$, and may therefore be expressed as

$$\pm(\lambda^2 + \beta^2)(\mu + \alpha) = 0;$$

that is,

$$\lambda^3 + \lambda^2\alpha + \lambda\beta^2 + \beta^2\alpha = 0, \quad (16)$$

where $-\alpha$ represents the third eigenvalue. Moreover, at the Hopf bifurcation, the two characteristic polynomials (12) and (16) are identical and therefore, equating their coefficients, we obtain three equations for the three unknowns β , α and φ ,

$$\alpha = 1 + \varphi + a\varphi, \quad \beta^2 = a\varphi + \varphi + a\varphi^2 - c; \quad \text{and} \quad \alpha\beta^2 = \varphi(ad - c),$$

that lead to equation

$$a(a+1)\varphi^3 + (3a+a^2+1)\varphi^2 + (a+1-ac-ad)\varphi - c = 0, \quad (17)$$

where the left hand side is the same as inequality (13). Equation (17) admits a unique positive solution $\bar{\varphi}$, as shown in the proof of proposition 4.2. The corresponding value of b , i.e., $b = b^*$, given by (15), is therefore the Hopf bifurcation point. \diamond

The value of b^* (or, equivalently, of $\bar{\varphi}$) may be found numerically. To give an example of determination of the exact value of b^* , we set

$$a = 5; \quad d = 2; \quad c = 1. \quad (18)$$

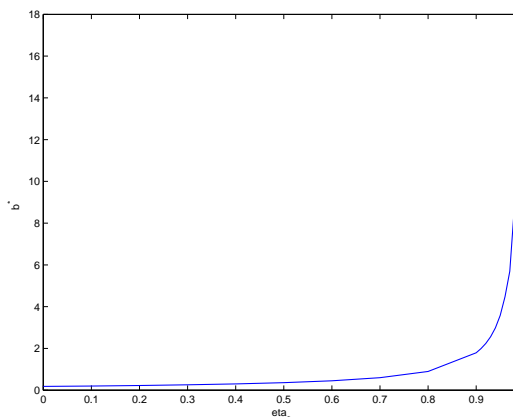


FIGURE 1. The function $b^* = b^*(\eta_c)$, which indicates how the bifurcation value b^* varies by varying the conversion rate η_c .

These values, which will be taken throughout the numerical investigations, have no real biological basis but are chosen simply to numerically illustrate the results contained in propositions 4.2 and 4.3.

From (17) we get

$$30\varphi^3 + 41\varphi^2 - 9\varphi - 1 = 0,$$

which, through simple algebra, leads to

$$\varphi_1 = 2\gamma_1 \cos \gamma - \frac{41}{90},$$

$$\varphi_2 = -\gamma_1 (\cos \gamma + \sqrt{3} \sin \gamma) - \frac{41}{90},$$

$$\varphi_3 = -\gamma_1 (\cos \gamma - \sqrt{3} \sin \gamma) - \frac{41}{90},$$

where $\gamma = -1/3 \arctan(\frac{45}{106586} \sqrt{2022855}) + 1/3 \pi$ and $\gamma_1 = \frac{1}{90} \sqrt{2491}$.

More explicitly, $\varphi_1 = \bar{\varphi} = 0.2622$, $\varphi_2 = -1.5466$ and $\varphi_3 = -0.0821$. Therefore $b^* = 0.17901(1 - \eta_c)^{-1}$. In correspondence to the value $\eta_c = 0.8$ we get $b^* = 0.8950$. This value is in agreement with our numerical investigations, as we will show in the next section.

5. Numerical investigations. In this section, we will show how the stability properties of the coexistence equilibrium E change by varying the positive parameter b , which we take as bifurcation parameter. We verify by numerical investigations that for fixed values of the parameters a , c , d and η_c a critical value of the parameter b exists, $b = b^*$, such that for $b > b^*$ the equilibrium E is a sink (a stable focus), whereas for $b < b^*$, it becomes a source (unstable focus), because a couple of complex conjugate eigenvalues of the Jacobian matrix $M(E)$, $\alpha \pm i\beta$, have crossed the imaginary axis. Moreover, as a consequence of the change of stability of E , a stable closed orbit O_E appears around this unstable fixed point. Numerical investigations fully agree with Propositions 4.2 and 4.3 and further clarify the nature of the Hopf bifurcation occurring at $b = b^*$, which is in fact of supercritical type.

According to (15), it is also possible to show that b^* depends on η_c : for decreasing values of η_c , the critical value b^* decreases. This means that higher values of η_c

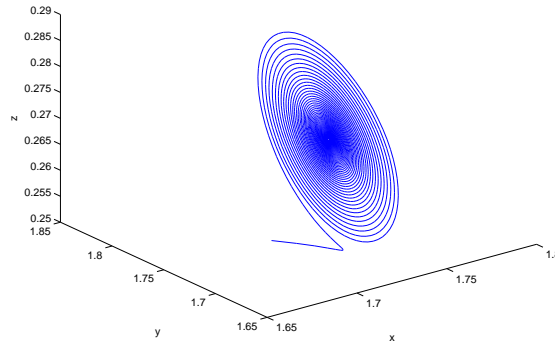


FIGURE 2. Case $b > b^*$, $b = 1$. System trajectories in the 3D phase space xyz for initial conditions near the stable focus E .

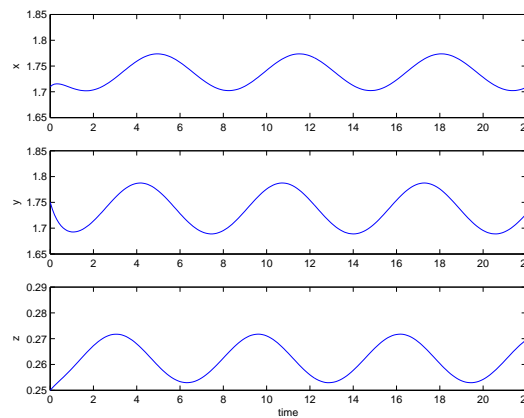


FIGURE 3. $b \approx b^*$. Variables versus time for initial conditions near the unstable focus E : the closed orbit O_E appears with period $P = 6.5614$.

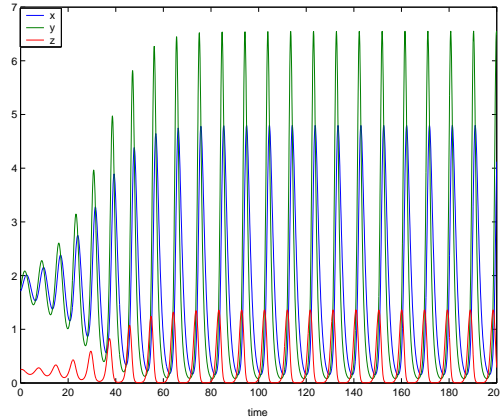
allow a larger range of b , $b < b^*$, for which the system exhibits sustained oscillations; see Fig.1.

Here we provide numerical investigations by assuming the theoretical values (18). In this case, the critical value of b at which the Hopf bifurcation occurs is found to be $b = b^* \approx 0.8950$. In the following, we describe and discuss system's phenomenology for values of b , which are representative of the cases $b > b^*$ and $b < b^*$, respectively. The simulations are performed by working in a MATLAB environment [17].

Case $b > b^$.* Set $b = 1$, which is representative of the case $b > b^*$. The equilibria E_0 and E_1 are both saddle points, whereas the coexistence equilibrium E is a stable focus. More precisely, taking initial conditions in the neighbourhood of E , system trajectories will tend to this stable fixed point in a way described by Fig. 2. The equilibria and the related stability properties are summarized in Table 1.

TABLE 1. Equilibria, eigenvalues and local stability for $b = 1$.

<i>Equilibrium</i>	<i>Eigenvalues</i>	<i>Local Stability</i>
$E_0 \equiv (0, 0, 0)$	$-1, -1, 2$	saddle
$E_1 \equiv (0, 0, 2)$	$-2, -1 \pm \sqrt{10}$	saddle
$E \equiv (1.73, 1.73, 0.27)$	$-2.5980, -0.0086 \pm i0.9657$	stable focus

FIGURE 4. Case $b < b^*$, $b = 0.1$. Time-dependent behaviour of system trajectories for initial conditions near the unstable focus E : the closed orbit O_E .

Case $b \approx b^$.* By decreasing the value of the bifurcation parameter, and precisely at $b \approx b^*$, a supercritical Hopf bifurcation occurs: E loses its stability and a stable closed orbit O_E appears around E .

As is well known from the Hopf Theorem [11], if $\pm i\beta$ denotes the complex conjugate eigenvalues of the Jacobian matrix that cross the imaginary axis, the period of the oscillation is given by $P = 2\pi/\beta$. Simulations shows that such an orbit arises with a period $P = 6.5614$, which is in agreement with the Hopf Theorem; see Fig. 3.

TABLE 2. Equilibria, eigenvalues and local stability for $b \approx b^*$.

<i>Equilibrium</i>	<i>Eigenvalues</i>	<i>Local Stability</i>
$E_0 \equiv (0, 0, 0)$	$-1, -1, 2$	saddle
$E_1 \equiv (0, 0, 2)$	$-2, -1 \pm \sqrt{10}$	saddle
$E \equiv (1.74, 1.74, 0.26)$	$-2.5732, \pm i0.9576$	non iperbolic

Case $b < b^$.* Set $b = 0.1$, which is representative of the case $b < b^*$. In this case we observe that E_0 and E_1 keep the same stability properties of the previous case, whereas the equilibrium E is now an unstable focus. Taking initial conditions in the neighbourhood of this point (i.e., the same initial conditions of the previous case), system trajectories will achieve the stable closed orbit O_E ; see Figures 4 and 5. In Table 3, the equilibria for this case and the related stability properties are summarized.

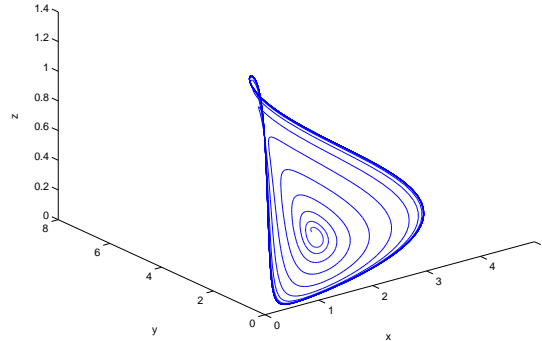


FIGURE 5. Case $b < b^*$, $b = 0.1$. System trajectories for initial conditions near the unstable focus E : the closed orbit O_E in the 3D phase space xyz .

TABLE 3. Equilibria, eigenvalues and local stability for $b = 0.1$.

<i>Equilibrium</i>	<i>Eigenvalues</i>	<i>Local Stability</i>
$O \equiv (0, 0, 0)$	$-1, -1, 2$	saddle
$E_0 \equiv (0, 0, 2)$	$-2, -1 \pm \sqrt{10}$	saddle
$E^* \equiv (1.79, 1.79, 0.21)$	$-2.3799, 0.0684 \pm i0.8825$	unstable focus

REMARK 2. We stress that in absence of cannibalism (i.e., for the case $b = 0$), the equilibrium E^* is an unstable focus, since the eigenvalues of the Jacobian matrix turn out to be $\lambda_1 = -2.3547$ and $\lambda_{2,3} = 0.0773 \pm i0.87087$. Moreover, for initial conditions in the neighbourhood of E^* , trajectories of the system again approach a periodic closed orbit.

6. Conclusions. Cannibalism is an interesting and important mechanism in population dynamics, as the large literature on the subject demonstrates [4]. In particular, its role in stabilizing or destabilizing population cycles has been deeply studied in the last years. The result is far to be unanimously accepted. The cases stressed in [22] are very persuasive: for example, Dieckmann et al. [9] found that population oscillations may be promoted by egg cannibalism and Hastings [13] found that cannibalism is destabilizing in his *Tribolium* model, whereas Desharnais and Liu in the same year showed in a *Tribolium* model that cannibalism is destabilizing [8]. Cushing first found both a stabilizing and a destabilizing effect of cannibalism in a discrete model [6] and then, for a size-structured model including cannibalism, he concluded that population oscillations are due mainly to age or size structure than cannibalism [7].

Therefore, the stabilizing-destabilizing effect of cannibalism appears to be strongly model dependent: it is not easy to draw general conclusions and a need of deeper investigation of cannibalism in various biological systems arises.

This paper is a contribution to the systematic investigation of cannibalism in predator-prey models. Our model is different from the ones recently proposed in [14] and [16], where a destabilizing effect of cannibalism has been detected, because

the variables are expressed in terms of number of individuals, and the adult-prey and adult-juvenile interactions consist in source uptake and conversion (through suitable yields) in new births. As a consequence, the number of adults varies only in cause of mortality and maturation from the juvenile class. This modelling approach avoids some shortcomings as the existence of a predator nonzero steady state in absence of prey.

The main result is that, in contrast to [14] and [16], we arrive essentially at the same conclusion of [15] and [22]: by using Hopf bifurcation analysis we prove that cycles are possible and that cannibalism suppresses these cycles; i.e., when cannibalism attack rate increases and passes a critical value, the coexistence steady state changes from unstable to stable.

Our model, as well as the earlier ones, is mainly a theoretical model which should be tested with specific real biological data rather than with qualitative population behaviour; however, we wish to state that the results obtained in this paper are not only of theoretical interest. The balance argument used in building model (1) is the same used in the context of microbial population models (see, e.g., [19]); therefore, the model seems particularly suitable to describe the growth of very small organisms, for example, cannibalistic copepods. As a matter of fact, some of the features detected in our model, such as the stabilizing role of cannibalism as well as decrease of the predator steady state with increasing a cannibalism attack rate, are observed phenomena in the simulation of the cyclopoid copepod *Cyclops abyssorum* (see, e.g., [23]).

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