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AN EVOLUTIONARY GAME-THEORETIC MODEL OF CANNIBALISM

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Abstract. Cannibalism, which functions as a life history trait in at least 1300 species of both invertebrates and vertebrates, plays important ecological and evolutionary roles in populations. During times of low resource availability, cannibalism of juveniles by adults can redirect reproductive energy to times of higher resource availability. For example, prolonged increases in sea surface temperature depress marine food webs and lead to increased egg cannibalism among glaucous-winged gulls (*Larus glaucescens*); consumption of a single cannibalized egg provides almost half the daily energy needs for an adult gull. Motivated by the glaucous-winged gull system, we use matrix models and bifurcation theory to investigate population and evolutionary dynamic consequences of adult-on-juvenile cannibalism. We show that in the presence of cannibalism, a population can survive under circumstances of low resource availability which, in the absence of cannibalism, lead to extinction. The evolutionary version of the model shows that cannibalism can be an evolutionarily stable strategy.

Key Words: Population dynamics, Allee effect, cannibalism, bifurcation, evolutionary dynamics, matrix models.

1. Introduction.

Cannibalism, the killing and eating of another member of the same species, functions as a life history trait in a wide variety of animals, including protozoans, invertebrates, and all the major vertebrate classes (Fox [1975], Elgar and Crespi [1992]). Even otherwise herbivorous animals such as leaf- and bark-eating insects engage in this behavior (Brower [1961], Beaver [1974], Richardson et al. [2010]), and at least 1300 species exhibit this trait (Polis [1981]).

Cannibalism plays important ecological and evolutionary roles in populations. It serves as a constraint on population size, favors the development of alternate life

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history strategies, complicates community dynamics, shapes social behavior, engenders the development of kin selection, lowers reproductive success, and may lead to complex nonlinear population dynamics including chaos (Davis and Dunn [1976], Polis [1981], Elgar and Crespi [1992], Stanback and Koenig [1992], Brouwer and Spaans [1994], Giray et al. [2001], Cushing et al. [2002]). Some individuals are genetically predisposed to exhibit this behavior (Park et al. [1961], Giray et al. [2001], Baker et al. [2014]) and geographically distinct populations may exhibit different cannibalism rates (Baker et al. [2014]). During times of low resource availability, cannibalism of juveniles by adults can redirect reproductive energy to times of higher resource availability (Elgar and Crespi [1992]), and cannibalism of juveniles may function as a "lifeboat" mechanism when resources are low and adults and juveniles are competing for the same or even different resources (Van den Bosch et al. [1988], Cushing [1991], Henson [1997]).

Cannibalism can result from overcrowding, stress, and the occurrence of unusual behavior patterns by vulnerable animals (Fox [1975]). Victim age, size, developmental stage, sex, and habitat may also contribute to its occurrence (Polis [1981], Baur and Baur [1986]). Poor food quality and lack of adequate food, however, constitute the most important reasons for cannibalism (Dong and Polis [1992]). For example, prolonged increases in sea surface temperature associated with El Niño-Southern Oscillation (ENSO) events depress marine food webs and lead adult Peruvian anchovy (*Engraulis ringens*) and Peruvian hake (*Merluccius gayi peruanus*) to cannibalize eggs and larvae at higher than usual rates (Alheit and Niquen [2004], Geurvara-Carrasco and Lleonart [2008]). Even human cannibalism in response to conditions of starvation has been reported (Brown [2013]).

Egg and chick cannibalism occurs commonly among colonial-nesting gulls (Paynter [1949], Tinbergen [1961], Patterson [1965], Drent [1970], Parsons [1971], Parsons [1975], Davis and Dunn [1976], Burger [1980]). A recent study demonstrated that egg cannibalism among glaucous-winged gulls (*Larus glaucescens*) and glaucous-winged × western gull (*L. glaucescens* × *occidentalis*) hybrids increased and hatching success decreased in response to impoverished food supplies resulting from ENSO-related high sea surface temperature events. Consumption of a single cannibalized egg provides almost half the daily energy needs for these birds (Hayward et al. [2014]). Although cannibalism may provide a benefit to individual gulls during times of environmental stress, it is not known whether cannibalism functions as an actual adaptive strategy during these times. This question motivates the present theoretical study.

Here, we investigate the population and evolutionary dynamic consequences of some key mechanisms involved in the cannibalism of immature individuals by adult individuals. Matrix models are particularly adept at describing the dynamics of populations structured into well-defined life cycle stages (Caswell [2001]). Our goal is to investigate the ways in which a low-dimensional matrix model that focuses on certain basic attributes of cannibalistic interactions can suggest plausible hypotheses concerning cannibalism as an adaptive life history strategy under environmental resource stress. We select the matrix model of the lowest possible dimension for these purposes: a two-stage juvenile–adult model in which the adult stage cannibalizes the juvenile stage (Cushing [1991], Henson [1997]). We also study an evolutionary version of the model. Since we are interested in changing environmental circumstances, a natural mathematical approach to the resulting dynamics is to use the methods of bifurcation theory. We will use this approach to demonstrate that a stable, nonextinction (positive) equilibrium of the evolutionary model can occur when cannibalism is present under circumstances for which only the extinction equilibrium is stable in the absence of cannibalism. The model also shows that cannibalism can be an evolutionarily stable strategy (ESS). The key biological and mathematical elements of our approach are the following:

- Cannibalism provides both negative and positive feedbacks in the density-dependent components of fitness. A positive feedback effect on fitness accrues to the cannibal by means of the nutrients obtained from the victim.
- Nonlinear matrix models that contain dominant positive feedback density effects at low population densities (component Allee effects; Courchamp et al. [2008]) and dominant negative feedback density effects at high population densities produce a backward bifurcation of positive (nonextinction) equilibria at $R_0 = 1$ and strong Allee effects for $R_0 < 1$. Here, R_0 is the net reproductive number at low population densities (i.e., in the absence of any density effects) (Cushing [1998], Cushing [2009], Cushing and Stump [2013], Cushing [2014]). This allows for population survival in a multiple attractor scenario when $R_0 < 1$ (due, for example, to low environmental resource availability).
- In the absence of positive feedback density effects (in particular, cannibalism), the bifurcation of positive (nonextinction) equilibria at $R_0 = 1$ is forward and the population goes extinct if $R_0 < 1$ (Cushing [1998], Cushing [2009], Cushing and Stump [2013]).

We describe this bifurcation-theoretic approach for a general juvenile–adult, population dynamic model in Section 2. In Section 3, we apply these bifurcation theory principles to study a juvenile–adult model that can include cannibalistic interactions between the adult and juvenile stages. The cannibalism efficiency of individual adults is measured by a parameter $v \geq 0$. We show, in a case of low environmental resource and hence $R_0 < 1$, that the population will go extinct when adults are not cannibalistic ($v = 0$), but can avoid extinction if adults are cannibalistic with sufficiently high intensity $v > 0$. This survival potential occurs because of a strong Allee effect created by a backward bifurcation that results from a positive feedback from cannibalism to adult survival. In Section 4, we look at an evolutionary version of the cannibalism model in which the cannibalism efficiency v of an individual adult is subject to Darwinian evolution. In that example, we consider a population that will go extinct because $R_0 < 1$ and because the mean level u of cannibalistic efficiency among its adults is too low (even zero). We show that if cannibalism efficiency is subject to Darwinian evolution, it can occur that evolution will select for a high enough mean level of adult cannibalistic efficiency so that the population avoids extinction, and that this mean is an "ESS."

2. Juvenile–adult matrix models. In this section, we set the theoretical framework for our study of a cannibalism model in Section 3. The lowest dimensional matrix model

$$x(t+1) = P(x(t))\, x(t) \tag{1}$$

for a population structured by juvenile and adult classes has 2×2 projection matrix

$$P(x) = \begin{pmatrix} 0 & p_{12}(x) \\ p_{21}(x) & p_{22}(x) \end{pmatrix}. \tag{2}$$

Here,

$$x = \mathrm{col}(x_1, x_2) = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$$

is a stage-structured demographic vector in which x_1 is the density of juveniles and x_2 is the density of adults. The time unit is the juvenile maturation period, which accounts for the 0 in the upper left corner of $P(x)$. The structure of this projection matrix is that of a (nonlinear) Leslie matrix in which $p_{12}(x)$ is adult fecundity, $p_{21}(x)$ is the fraction of surviving (and hence maturing) juveniles, and $p_{22}(x)$ is the fraction of surviving adults during one unit of time. These vital rates are, as indicated, assumed to be density-dependent.

Let R^2 denote two-dimensional Euclidean space and let

$$R_+^2 = \left\{x \in R^2 : x_i > 0\right\}, \quad \bar{R}_+^2 = \left\{x \in R^2 : x_i \geq 0\right\}, \quad \partial R_+^2 = \bar{R}_+^2 \backslash R_+^2$$

denote the positive cone, its closure, and its boundary, respectively. We assume that the entries in $P(x)$ satisfy the following conditions:

A1: There is an open set $\Omega \subseteq R^2$ containing $\bar{R}_+^2$ on which the entries $p_{ij}(x)$ are twice continuously differentiable and satisfy $p_{12}(x) > 0$ and $0 < p_{21}(x)$, $p_{22}(x) < 1$ for all $x \in \Omega$.

The projection matrix (2) is primitive for $x \in \bar{R}_+^2$. The strictly dominant eigenvalue of $P(x)$ is

$$r(x) \mathrel{\mathring{=}} \frac{1}{2}\left(p_{22}(x) + \sqrt{p_{22}^2(x) + 4p_{12}(x)\,p_{21}(x)}\right).$$

Let

$$R_0(x) \mathrel{\mathring{=}} p_{12}(x)\,\frac{p_{21}(x)}{1 - p_{22}(x)}.$$

The quantities $r(x)$ and $R_0(x)$ are the population growth rate and net reproductive number (expected number of juveniles produced per juvenile per life time), respectively, under the assumption that the population is held fixed at x. For notational simplification, we denote the inherent (i.e., density-independent) population growth rate and net reproductive number by

$$r = r(0) \quad \text{and} \quad R_0 = R_0(0),$$

respectively. We also use a superscript 0 to denote evaluation at $x = 0$. For example,

$$p_{ij}^0 \mathrel{\mathring{=}} p_{ij}(0), \quad \partial_k^0 p_{ij} = \left.\frac{\partial p_{ij}(x)}{\partial x_k}\right|_{x=0}.$$

Note that $r = 1$ if and only if $R_0 = 1$ (see Cushing and Zhou [1994]), i.e., if and only if $1 - p_{22}^0 = p_{12}^0 p_{21}^0$. Left and right eigenvectors $w_L, w_R \in R_+^2$ of $P(0)$ associated with $r = 1$ are

$$w_L^T = \frac{1}{1 + p_{12}^0 p_{21}^0}\begin{pmatrix} p_{21}^0 & 1 \end{pmatrix} \quad \text{and} \quad w_R = \begin{pmatrix} p_{12}^0 \\ 1 \end{pmatrix}.$$

The quantity

$$\kappa \mathrel{\mathring{=}} -w_L^T\left(\nabla^0 p_{ij} w_R\right) w_R, \quad \nabla^0 p_{ij} = \begin{pmatrix} \partial_1^0 p_{ij} & \partial_2^0 p_{ij} \end{pmatrix}$$

will be important for us when evaluated at $r = 1$ (equivalently $R_0 = 1$). A calculation shows

$$(3) \quad \kappa = -\frac{p_{21}^0\left[p_{12}^0 \partial_1^0 p_{12} + \partial_2^0 p_{12}\right] + p_{12}^0\left[p_{12}^0 \partial_1^0 p_{21} + \partial_2^0 p_{21}\right] + \left[p_{12}^0 \partial_1^0 p_{22} + \partial_2^0 p_{22}\right]}{1 + p_{12}^0 p_{21}^0}$$

when $R_0 = 1$.

A *positive* (or *nonnegative*) *equilibrium* is a fixed point of the map (1) that lies in R_2^+ (or $\bar{R}_2^+$). We refer to the equilibrium $x = 0$ as the *extinction equilibrium.* We consider these equilibria as they depend on r (or R_0). If x is an equilibrium that exists for a specified value of r (or R_0), then we refer to (r, x) (or (R_0, x)) as an *equilibrium pair.* If x is a positive (nonnegative) equilibrium, then we refer to the equilibrium pair as *positive (nonnegative).* Note that $(r, 0)$ (or $(R_0, 0)$) is an equilibrium pair for all values of r (or R_0); we refer these as *extinction equilibrium pairs.* The following facts are known about nonlinear matrix models with primitive projection matrices, and therefore, about the juvenile–adult model (1)–(2) (Cushing [1998], Cushing [2009]). The statements are valid for both equilibrium pairs (x, r) and (x, R_0).

The set of positive equilibrium pairs of (1)–(2) contains a (maximal) continuum $\mathcal{C}$ with the following properties:

- $(1, 0) \in \overline{\mathcal{C}}$ (i.e., the continuum $\mathcal{C}$ bifurcates from $(1, 0)$);
- $\mathcal{C} \subset R_+ \times R_+^2$ (i.e., the continuum $\mathcal{C}$ consists of positive equilibrium pairs corresponding to positive values of r (or R_0));
- $\mathcal{C}$ is unbounded in $R_+ \times R_+^2$.

These facts derive fundamentally from the well-known Rabinowitz alternative in bifurcation theory (Rabinowitz [1971]; see also Keilhöfer [2004]). The bifurcation at the extinction equilibrium when $R_0 = 1$ is a transcritical bifurcation, and therefore we typically expect an exchange of stability to occur between the continuum of extinction pairs and the positive equilibria on $\mathcal{C}$ (Keilhöfer [2004]). This, indeed, occurs for matrix models. We say that a *backward* or *forward bifurcation* occurs if there exists a neighborhood $\mathcal{N}$ of $(1, 0)$ such that $(r, x) \in \mathcal{N} \cap \mathcal{C}$ implies $r < 1$ or $r > 1$, respectively (equivalently $R_0 < 1$ or $R_0 > 1$). We say that the bifurcation is *stable* (respectively, *unstable*) if the positive equilibrium pairs in the neighborhood are (locally asymptotically) stable (respectively, unstable). The following fundamental bifurcation theorem is proved in Cushing [1998]:

> The extinction equilibrium pair is (locally asymptotically) stable if $r < 1$ and unstable if $r > 1$ (equivalently $R_0 < 1$ or $R_0 > 1$). Suppose $\kappa \neq 0$. Then, in a neighborhood of the bifurcation point $(1, 0)$, the direction of bifurcation determines the stability of the bifurcation:

- the bifurcation at $r = R_0 = 1$ is unstable if it is backward and stable if it is forward;
- the bifurcation at $r = R_0 = 1$ is backward if $\kappa < 0$ and forward if $\kappa > 0$.

Note 1. When $r > 1$ (equivalently $R_0 > 1$), the extinction equilibrium is not only unstable, but the matrix model is uniformly persistent with respect to ∂R_+^2

(Cushing [1998], Kon et al. [2004]). In this case, no orbits in the positive cone tend to 0 as $t \to +\infty$. ■

Note 2. The stability properties described above are obtained by the linearization principle. The stable equilibria are hyperbolic. ■

The direction of bifurcation is determined by the sign of κ and hence by the partial derivatives of the matrix entries p_{ij} with respect to the components of x, all evaluated at $x = 0$ and $r = R_0 = 1$. A negative derivative $\partial^0_{x_k} p_{ij} < 0$ means that a *negative feedback* mechanism is in play at low densities, whereas a positive derivative $\partial^0_{x_k} p_{ij} > 0$ means the presence of a *positive feedback* mechanism at low densities, which is called a *component Allee effect* (Courchamp et al. [2008]). If only negative feedback mechanisms are present in a model (as is often the case), then clearly, $\kappa > 0$ (there is no need to actually calculate κ) and a forward and hence stable bifurcation occurs as r (equivalently R_0) increases through 1.

Note 3. If only negative feedback effects are present in the model, or more generally, if $p_{ij}(x) \leq p^0_{ij}$ for all $x \in \bar{R}^2_+$, then $r < 1$ (equivalently $R_0 < 1$) implies that $x = 0$ is globally asymptotically stable with respect to nonnegative initial conditions (Cushing [1998]). In other words, extinction is assured if $r < 1$ (equivalently $R_0 < 1$). ■

Necessary, but not sufficient, for a backward bifurcation is the presence of some component Allee effects. If the component Allee effects are of sufficient magnitude (compared to the negative feedback mechanisms present) at low densities so that $\kappa < 0$, then a backward and hence unstable bifurcation occurs.

We say a *strong Allee effect* occurs in a model if there exists both a positive and an extinction attractor. Thus, a necessary condition for a strong Allee effect is that $r < 1$ or equivalently that $R_0 < 1$.

An example of a strong Allee effect is when, in addition to a stable extinction equilibrium, there also exists a stable positive equilibrium. If a backward bifurcation occurs, then there do exist positive equilibria for $r < 1 (R_0 < 1)$, namely, those from the bifurcating continuum $\mathcal{C}$. However, in a neighborhood of the extinction equilibrium $(1, 0)$, the bifurcating positive equilibria from $\mathcal{C}$ are unstable. Strong Allee effects, with respect to positive equilibria, usually occur in population models because the backward bifurcating continuum $\mathcal{C}$ "turns back to the right" and thereby creates multiple positive equilibria for values of r and $R_0 < 1$. The reason for this is that population models generally include negative feedback mechanisms at high densities. See Figure 1b for a schematic representation of such a bifurcation diagram. This phenomenon implies a potential for a strong Allee effect, since it creates multiple positive equilibria for $r < 1$ (equivalently $R_0 < 1$). One obvious criterion sufficient for this to occur is the existence of a positive equilibrium pair from the continuum $\mathcal{C}$ associated with $r = 1$ (equivalently $R_0 = 1$). In that case, there is an interval of r (equivalently R_0) values less than 1 (with 1 as its upper end point) on which there exist at least two positive equilibria, one of which is on

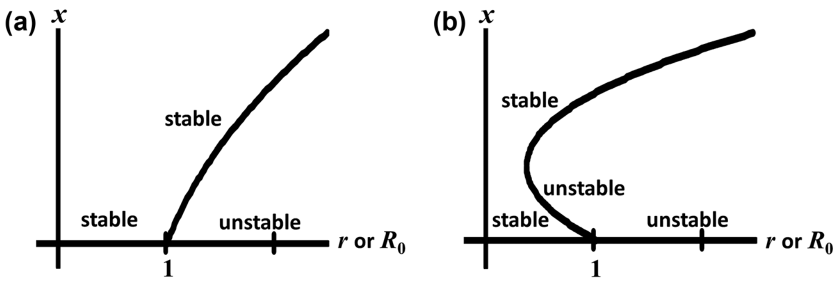

FIGURE 1. Schematic representations are shown for the two basic (transcritical) bifurcations that occur at the extinction equilibrium $x = 0$ in nonlinear matrix models as r (equivalently R_0) increases through 1. (a) A forward (right or supercritcal) bifurcation of positive equilibria x occurs if $\kappa > 0$ and the bifurcating positive equilibria are stable (at least in a neighborhood of the bifurcation point). (b) A backward (left or subcritical) bifurcation of positive equilibria x occurs if $\kappa < 0$ and the bifurcating positive equilibria are unstable (at least in a neighborhood of the bifurcation point). Because of assumed negative effects at high densities, the bifurcating continuum $\mathcal{C}$ of positive equilibria "turns around" at a value of r (or R_0) less than 1. This is generally a saddle-node bifurcation, which usually (but not always) results is a branch of stable positive equilibria as indicated. This creates an interval of r (equivalently R_0) values less than 1 on which a strong Allee effect occurs.

the branch of unstable equilibria that bifurcates from the extinction equilibria. An analytic criterion sufficient to guarantee this is given in Cushing [2014]. It involves establishing an *a priori* bound on positive equilibria in terms of r or R_0.

A2: Suppose there exists a function $m : R_+ \to R_+$ which is bounded on compact intervals of R_+ such that

$$\|x\| \triangleq |x_1| + |x_2| \leq m(r) \text{ or } m(R_0)$$

for all positive equilibrium pairs $x \in R^2_+$ of (1)–(2).

Theorem 1. *(Cushing [2014]). Assume A1 and $\kappa < 0$. If there exists a positive equilibrium for $r = R_0 = 1$ (which occurs if A2 holds), then there exist, in addition to a stable extinction equilibrium, at least two positive equilibria of the juvenile–adult matrix model (1)–(2) for $r \lessapprox 1$ (equivalently $R_0 \lessapprox 1$), one of which is unstable.*

While the conditions of Theorem 1 imply the potential for a strong Allee effect, it is necessary for a strong Allee effect that one of the positive equilibria be stable. This is model-dependent and might or might not occur (Cushing [2014]). However, when the continuum $\mathcal{C}$ "turns around," it usually does so at a saddle-node bifurcation (sometimes called a blue sky or tangent bifurcation). Saddle-node bifurcations generally involve the collision of unstable and stable equilibria. Therefore, one can usually expect that a strong Allee effect will occur under the circumstances of

Theorem 1. We will see that this is, indeed, the case in the juvenile–adult cannibalism model studied in the next section.

3. A juvenile–adult cannibalism model.

In this section, we adapt the general juvenile–adult model (1)–(2) to account for cannibalism on juveniles by adults and apply the results of Theorem 1. We focus on the effects of cannibalism on the survival probabilities p_{21} and p_{22} of juveniles and adults, respectively.

In the absence of cannibalism, we assume that survival probabilities and fecundity are functions of the amount of noncannibalistic food resources $\rho \geq 0$ available in the habitat:

$$p_{12} = b(\rho), \quad p_{21} = s_1(\rho), \quad p_{22} = s_2(\rho),$$

where $b(\rho) > 0$ and the fractions $s_i(\rho)$ are all increasing functions of ρ. We assume $b(0) = 0$, that is to say, that reproduction fails in the absence of the resource ρ.

In the presence of juvenile cannibalism by adults, juvenile survival p_{21} is modified by the probability that a juvenile survives cannibalism, i.e.,

$$p_{21}(x_1, x_2, \rho) = s_1(\rho)\left(1 - p(x_1, x_2, \rho)\, x_2\right).$$

The fraction $p(x_1, x_2, \rho)x_2$ is the probability a juvenile is cannibalized in the presence of x_2 adults and x_1 juveniles, and hence, $1 - p(x_1, x_2, \rho)x_2$ is the probability of a juvenile surviving under these circumstances.

We assume that the probability of a juvenile being cannibalized increases as the number of adults increases, i.e., the fraction $p(x_1, x_2, \rho)x_2$ is an increasing function of $x_2 \geq 0$. On the other hand, the fraction $p(x_1, x_2, \rho)x_2$ is a decreasing function of x_1, as a result of the familiar prey (or, in this case, victim) saturation effect in response to predation (cannibalism). Finally, we assume that $p(x_1, x_2, \rho)x_2$ is a decreasing function of ρ, that is to say, cannibalism decreases if the noncannibalistic food resource availability increases.

The other effect of cannibalism we place in the model is an increase in the adult cannibal survival probability that accrues from its victims. (We ignore, in this model, benefits that might accrue to adult fecundity.) To do this, we modify adult survival probability s_2 by a factor so that

$$p_{22}(x_1, x_2, \rho) = s_2(\rho)\, \sigma(w),$$

where

$$w \triangleq p(x_1, x_2, \rho)\, x_1$$

is the number of juveniles cannibalized per adult. In the absence of cannibalism, we assume in this model that population regulation is by means of adult regulation of fecundity, namely, per adult fecundity $b(\rho)$ is modified by a factor $\varphi(x_2)$ that is dependent on adult density x_2 :

$$p_{12}\left(x, x_2\right) = b\left(\rho\right)\varphi\left(x_2\right).$$

In summary, we have the juvenile–adult model (1) with the projection matrix

$$P\left(x\right) = \begin{pmatrix} 0 & b\left(\rho\right)\varphi\left(x_2\right) \\ s_1\left(\rho\right)\left(1 - p\left(x_1, x_2, \rho\right)x_2\right) & s_2\left(\rho\right)\sigma\left(p\left(x_1, x_2, \rho\right)x_1\right) \end{pmatrix}. \tag{4}$$

The mathematical assumptions we make (in addition to the general requirements on the entries p_{ij} in A1) are the following:

- **Inherent vital rates:** $b(\rho)$ and $s_i(\rho)$ are increasing continuous functions of ρ on an open interval I containing $\bar{R}_+$ which satisfy $b(0) = 0$ and $b(\rho) \geq 0$, $0 < s_i(\rho) \leq 1$ for $\rho \geq 0$.
- **Population regulation in the absence of cannibalism:** $\varphi(x_2)$ is a continuously differentiable and nonincreasing function of x_2 on I which satisfies

  $$\varphi\left(0\right) = 1, \varphi'\left(0\right) < 0,\ \varphi\left(x_2\right) \geq 0 \text{ for } x_2 \geq 0.$$

  Assume $\varphi(x_2)x_2$ is bounded, i.e., there is a constant $\varphi_0 > 0$ such that

  $$\varphi\left(x_2\right)x_2 \leq \varphi_0 \text{ for } x_2 \geq 0.$$

- **Cannibalism interactions:**

  (1) $p(x_1, x_2, \rho)x_2$ is a continuous function on $\Omega \times I$ that is twice continuously differentiable in x_1 and x_2 and that satisfies the following conditions for $\rho \geq 0$ and $x_i \geq 0$:

  $$0 \leq p\left(x_1, x_2, \rho\right)x_2 \leq 1$$
  $$p\left(x_1, x_2, \rho\right)x_2 \text{ increasing in } x_2 \text{ and decreasing in both } x_1 \text{ and } \rho.$$

  (2) $\sigma(w)$ is twice continuously differentiable on I, is nondecreasing for $w \geq 0$, and satisfies

  $$\sigma\left(0\right) = 1, \quad \sigma'\left(0\right) > 0, \quad 0 < s_2\left(\rho\right)\sigma\left(w\right) \leq \sigma_0\left(\rho\right) < 1$$

  for $\rho, w \geq 0$ and some constant $\sigma_0(\rho)$.

The bifurcation alternatives described in Section 2 apply to the juvenile–adult model (1) with projection matrix (4). The direction of bifurcation (and hence the stability) of the positive equilibria that bifurcate at $R_0(\rho) = 1$, where

$$R_0(\rho) = b(\rho)\frac{s_1(\rho)}{1 - s_2(\rho)},$$

is determined by the sign of κ as given by the formula (3), which for the projection matrix (4) is

$$\kappa = \frac{1}{s_1(\rho)}\frac{1 - s_2(\rho)}{2 - s_2(\rho)}\left(\left[s_1(\rho) - s_2(\rho)\sigma'(0)\right]p(0,0,\rho) - s_1(\rho)\varphi'(0)\right).$$

Notice that the sign of κ is ambiguous under the monotonicity assumptions made on φ and σ. The term

$$-s_1(\rho)\varphi'(0) > 0$$

is positive while the sign of the term

$$\left[s_1(\rho) - s_2(\rho)\sigma'(0)\right]p(0,0,\rho) \tag{5}$$

depends on that of the bracketed factor.

If cannibalism is absent, i.e., if $p(x_1, x_2, \rho) \equiv 0$ or if the benefit of cannibalism to adult survival is weak, i.e., $\sigma'(0)$ is small, then $\kappa > 0$ and the bifurcation at $R_0(\rho) = 1$ is forward. Note that $R_0(0) = 0$ and therefore $R_0(\rho)$ will be less than 1 when resource availability ρ is low. Moreover, when $R_0(\rho) < 1$, Note 4 in Section 2 applies and the extinction equilibrium $x = 0$ is globally asymptotically stable (with respect to nonnegative initial conditions). This means that there is no chance of survival if $R_0(\rho) < 1$, i.e., if the resource ρ is low.

We are interested in a backward bifurcation and the potential for a strong Allee effect, in order to have the possibility of nonextinction when $R_0(\rho) < 1$. A backward bifurcation ($\kappa < 0$) occurs if (and only if) the term (5) is sufficiently negative. This occurs when $p(0, 0, \rho) > 0$ and when $\sigma'(0)$ is large. The meaning of these mathematical conditions is, respectively, that cannibalism must be present (at low population densities) and that the benefit of cannibalism to adult survival must be sufficiently large. To obtain the potential for a strong Allee effect by means of Theorem 1, we have remaining the establishment of the equilibrium *a priori* bound in A2. From the equilibrium equations, for positive equilibria, we have

$$0 \le x_1 \le R_0(\rho)\frac{1 - s_2(\rho)}{s_1(\rho)}\varphi_0$$

$$0 \leq x_2 \leq s_1(\rho)\, x_1 + \sigma_0(\rho)\, x_2 .$$

The second inequality implies

$$0 \leq x_2 \leq R_0(\rho) \frac{1 - s_2(\rho)}{1 - \sigma_0(\rho)} x_1 \leq R_0^2(\rho) \frac{(1 - s_2(\rho))^2 \varphi_0}{(1 - \sigma_0)\, s_1(\rho)},$$

and hence A2 holds with

$$m(R_0(\rho)) = R_0(p) \frac{1 - s_2(\rho)}{s_1(\rho)} \varphi_0 + R_0^2(\rho) \frac{(1 - s_2(\rho))^2 \varphi_0}{(1 - \sigma_0(\rho))\, s_1(\rho)}.$$

By Theorem 1, we conclude that for an interval $R_0^{\min} \leq R_0(\rho) < 1$ of $R_0(\rho)$ values, there exist, in addition to the stable extinction equilibrium, at least two positive equilibria, one of which is unstable. What remains to prove is that there is a stable positive equilibrium for these $R_0(\rho)$ values. Unfortunately, we do not have a general criterion that guarantees the stability of a positive equilibrium (or any other positive nonextinction attractor). We can, however, illustrate that a strong Allee effect can occur in the model (1)–(4) by means of specific examples and numerical studies.

For this purpose, we utilize some specific formulas for the model coefficients that satisfy the required conditions for Theorem 1 (assumptions A1 and A2). We utilize rational functions of types commonly used in population dynamics (such as Holling type II and Beverton–Holt functionals).

We model the probability that a juvenile is cannibalized by

$$p(x_1, x_2, \rho)\, x_2 = \frac{1}{1 + c_4 \rho} \frac{1}{1 + c_1 x_1} \frac{v x_2}{1 + v x_2}. \tag{6}$$

The derivative (sensitivity) of $p(x_1, x_2, \rho)x_2$ with respect to x_2 evaluated at $x = 0$, namely,

$$\frac{1}{1 + c_4 \rho} v,$$

is a measure of adult cannibal aggressiveness (at low population densities) in that it measures the increase in the probability a juvenile is cannibalized that results from an increase in the number of cannibals. Note that this model assumes that cannibalism aggressiveness is inversely related to the amount ρ of noncannibal resource available and that v is the maximal aggressiveness, which occurs when the resource ρ vanishes. We will say simply that v is *cannibalism aggressiveness*. The model (6) also assumes a cannibalism saturation effect, which is modeled by a Holling-II-type functional of cannibal density x_2.

We assume that the consumption (or capture) of the noncannibalistic resource ρ also follows a saturating, Holling-II-type functional

$$\frac{c_4\rho}{1+c_4\rho},$$

and assume that inherent adult fecundity and survival and inherent juvenile survival are each proportional to this consumed amount of noncannibalism resource, as follows:

First, we assume that inherent adult fecundity is described by

$$b(\rho)=\beta e^{-c_5 v}\frac{c_4\rho}{1+c_4\rho}. \tag{7}$$

This assumes efforts expended toward cannibalism decrease efforts toward obtaining noncannibalistic resources. Here, β is the maximal possible inherent fecundity. We also assume that adult fecundity is regulated by the density of adults according to the discrete logistic (or Beverton–Holt) functional:

$$\varphi(x_2)=\frac{1}{1+c_2x_2}. \tag{8}$$

Second, we assume that adult survival $s_2(\rho)\sigma(p(x_1,x_2,\rho)x_1)$ is described by the expressions:

$$s_2(\rho)=\left[s_2^0+\left(s_2^m-s_2^0\right)\left(1-e^{-c_6 v}\right)\right]\frac{c_4\rho}{1+c_4\rho}, \tag{9}$$

$$\sigma(w)=\frac{(1+\gamma)(1+c_3w)}{1+\gamma+c_3w}. \tag{10}$$

These embody two assumptions with regard to how adult survival depends on cannibalism. It assumes that more aggressive cannibals have a higher inherent survival probability. This accounts for the bracketed factor in $s_2(\rho)$, which is an increasing function of v from the low level of s_2^0 (in the absence of cannibalism) to a highest level of $s_2^m>s_2^0$. It also assumes that the number of juveniles $w=p(x_1,x_2,\rho)x_1$ cannibalized by an adult increases its survival probability by the factor $\sigma(w)$. This factor is an increasing function of w that ranges from a low of 1 to a high of $1+\gamma$.

Finally, we assume that inherent juvenile survivorship is proportional to the consumed noncannibalism resource

$$s_1(\rho) = s_1^0 \frac{c_4 \rho}{1 + c_4 \rho}. \tag{11}$$

Here, s_1^0 is the maximum possible inherent juvenile survival probability.

These model specifications require for the coefficients appearing in (6)–(11) that

$$0 < s_1^0 < 1, \quad 0 < s_2^0 < s_2^m < 1, \quad s_2^m (1 + \gamma) \leq 1$$
$$v \geq 0, \quad c_i \geq 0.$$

We note that cannibalism is absent in the model population if $v = 0$. We also note that this model contains a trade-off due to cannibalism activity, namely, *a higher level of cannibalism aggressiveness v increases adult survival, but decreases adult fecundity.*

Table 1 contains a summary of the biological interpretations of the model coefficients in this example.

In this example,

$$p(0, 0, \rho) = \frac{v}{1 + c_4 \rho}, \quad \sigma'(0) = c_3 \frac{\gamma}{1 + \gamma}.$$

From our remarks above (derived from and appearing after (5)), we see that a backward bifurcation occurs in this model if $v > 0$ (cannibalism occurs), $\gamma > 0$ (there is a positive benefit of cannibalism to adult survival), and c_3 is sufficiently large (adult survival is sufficiently responsive to cannibalism aggressiveness).

To be more explicit about the parameter relationships that lead to a backward bifurcation in this example, we calculate

$$\kappa = \frac{1}{s_1(\rho)} \frac{1 - s_2(\rho)}{2 - s_2(\rho)} \left[s_1(\rho) c_2 + \left(s_1(\rho) - s_2(\rho) \frac{\gamma}{1 + \gamma} c_3 \right) \frac{1}{1 + c_4 \rho} v \right].$$

From this expression, we see that a backward bifurcation occurs if the bracketed term is negative, a constraint we can write (using (11) and (9)) as

$$c_2 (1 + c_4 \rho) < \left(\frac{s_2^0}{s_1^0} \frac{\gamma}{1 + \gamma} c_3 - 1 \right) v. \tag{12}$$

From this inequality, we can see the key mechanisms in this model that promote a backward bifurcation (given the necessary condition that there exists a benefit of cannibalism to adult survival $\gamma > 0$): the benefit to adult survival is high (c_3 is large); inherent juvenile survival is low (s_1^0 is small); and cannibalism aggressiveness

TABLE 1. Biological Interpretations of Parameters.

Parameter	Interpretation
v	cannibalism aggressiveness
c_1	effectiveness of victim saturation in reducing probability of cannibalism
c_2	adult regulation of adult fecundity
c_3	measures response of adult survival to an increase in the number of juveniles cannibalized
c_4	inverse of the half-saturation level of the Holling-II-type resource uptake rate
c_5	measures rate of decrease in inherent adult fecundity due to an increase in cannibalism intensity
c_6	measures rate of increase in inherent adult survival due to an increase in cannibalism intensity
β	maximum adult fecundity in the absence of cannibalism as a function of resource availability
γ	maximum relative gain in adult survival due to cannibalism
s_1^0, s_2^0	maximum juvenile and adult survival as functions of resource availability (in the absence of cannibalism)
$s_2^m(1+\gamma)$	maximal adult survival in the presence of cannibalism

is high (v is large). Working against a backward bifurcation is a high level of food resource ρ, a high resource uptake rate c_4, and strong density regulation of fecundity by adult density (large c_2).

In this example,

$$R_0(\rho) = \beta s_1^0 e^{-c_5 v} \left(\frac{c_4 \rho}{1 + c_4 \rho} \right) \left(\frac{c_4 \rho}{1 + c_4 \rho - \left(s_2^0 + \left(s_2^m - s_2^0 \right) \left(1 - e^{-c_6 v} \right) \right) c_4 \rho} \right)$$

is an increasing function of ρ satisfying

$$R_0(0) = 0, \quad R_0(+\infty) = \beta s_1^0 e^{-c_5 v} \frac{1}{1 - \left(s_2^0 + \left(s_2^m - s_2^0 \right) \left(1 - e^{-c_6 v} \right) \right)}.$$

Thus, $R_0(\rho) < 1$ for low resource levels ρ. If $R_0(+\infty) > 1$, then $R_0(\rho) > 1$ for high resource levels ρ. Otherwise, $R_0(\rho)$ never rises above 1 for any level of resource availability ρ.

Figure 2 shows simulations of this model that illustrate a strong Allee effect arising from a backward bifurcation caused by the positive feedbacks from cannibalism. Figures 1a and b show, respectively, a sample orbit for a noncannibalistic population ($v = 0$) in a favorable environment (value of ρ for which $R_0(\rho) > 1$) and in an unfavorable environment (value of ρ for which $R_0(\rho) < 1$). Because only negative feedbacks are in force in the absence of cannibalism, the bifurcation at $R_0(\rho) = 1$ is forward and stable. As expected, Figure 2a shows population survival and equilibration to a positive equilibrium, while Figure 2b shows population extinction. In the latter case, if the population were to adopt cannibalism ($v > 0$), all other parameters remaining the same, Figure 2c shows the population no longer goes extinct; specifically, the population equilibrates to a positive equilibrium. This survival is initial-condition-dependent, however (i.e., there is a strong Allee effect). This is illustrated by Figure 2d in which only the initial condition is changed and extinction results.

4. Evolutionary dynamics. The juvenile–adult model in Section 2 and the cannibalism version in Section 3 are time autonomous models in that they assume that the entries in the projection matrix do not depend explicitly on time t. There are, however, numerous reasons why one might want to study cases when these entries, or more specifically when the vital rates describing survival, fecundity, and so on, change over time, due, for example, to stochastic fluctuations or regular (e.g., seasonal) oscillations. In this section, we consider the case in which the entries in the projection matrix change over time due to Darwinian natural selection.

We briefly describe an evolutionary game-theoretic version of the juvenile–adult model (1)–(2) and describe some recent theoretical results with regard to how the

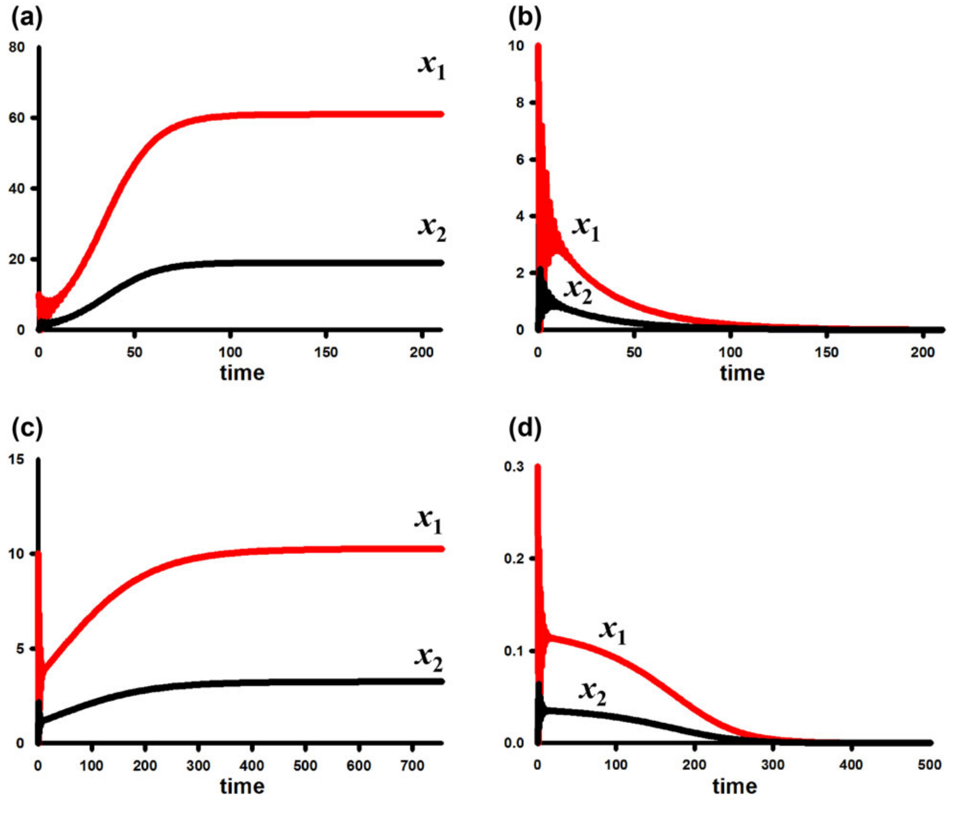

FIGURE 2. Sample time series generated by the juvenile–adult model (1)–(4) with expressions (6)–(11). All cases use parameter values $\beta = 4$, $s_1^0 = s_2^0 = 0.25$, $s_2^m = 0.50$, $c_1 = c_2 = c_4 = c_5 = 0.01$, $c_3 = 10$, $c_6 = 0.04$, and $\gamma = 0.9$. Simulations were computed for 10,000 time steps. (a) Cannibalism absent ($v = 0$) and high resource level $\rho = 2000$, which imply $R_0(2000) \approx 1.19 > 1$: the population survives and equilibrates to $(x_1, x_2) \approx (61.0, 19.0)$ from initial condition $(x_1, x_2) = (10, 0)$. (b) Cannibalism absent ($v = 0$) and low resource level $\rho = 600$, which imply $R_0(600) \approx 0.935 < 1$: the population goes extinct from initial condition $(x_1, x_2) = (10, 0)$. (c) Cannibalism present ($v = 5$) and low resource level $\rho = 600$, which imply $R_0(600) = 0.936 < 1$: the population survives and equilibrates to $(x_1, x_2) \approx (10.3, 3.25)$ from initial condition $(x_1, x_2) = (10, 0)$. (d) Cannibalism present ($v = 5$) and low resource level $\rho = 600$, which imply $R_0(600) = 0.936 < 1$: the population goes extinct from initial condition $(x_1, x_2) = (0.3, 0)$.

fundamental bifurcation theorem described in Section 2, in particular the relationship between stability and the direction of bifurcation of positive equilibria, extend to the evolutionary model. We are particularly interested, as we were in the nonevolutionary model, in backward bifurcations and potential strong Allee effects that occur when cannibalism aggressiveness increases in response to low noncannibalistic resource levels.

As an example, we look briefly at the evolutionary version of the example in Section 3 when the cannibalism intensity coefficient v is subject to Darwinian evolution. This will allow us to consider conditions under which the adoption of cannibalism is an ESS, even for a population that is initially noncannibalistic, when faced with a shortage of environmental food resource ρ.

The entries in the projection matrix are per capita vital rates. We assume that the rates associated with a focal individual (sometimes referred to as a mutant) are determined by a phenotypic trait v that has a heritable component and, in some circumstances, by the traits of all other individuals as represented by the mean trait u. Thus, the projection matrix $P(x,v,u)$ and its dominant eigenvalue $r(x,v,u)$ are functions of x, v, and u. The methodology of evolution game theory asserts that the dynamics of x and u are described by the equations (Vincent and Brown [2005], McGill and Brown [2007]):

$$x\,(t+1) = \left. P\,(x\,(t)\,, v, u\,(t))\right|_{v=u(t)} x\,(t) \tag{13a}$$

$$u\,(t+1) = u\,(t) + \theta^2 \left. \frac{\partial \ln r(x(t),v,u(t))}{\partial v} \right|_{v=u(t)} . \tag{13b}$$

In some derivations of these dynamic equations, $\theta^2 \geq 0$ is a constant of proportionality related to the variance of the trait v, which is assumed constant over time. The constant θ^2 measures the speed of evolution (in particular, evolution is absent if $\theta^2 = 0$). In this model, $\ln r(x,v,u)$ is taken as fitness. The trait dynamic equation (13b) has a long history in evolutionary modeling (e.g., in population genetics related to the additive genetic variance assumption). It is sometimes referred to as the breeder's equation, Fisher's equation of additive genetic variance, Lande's equation, or the canonical equation of adaptive dynamics (Lande [1976], Abrams et al. [1993], Dieckmann and Law [1996], Abrams [2001], Abrams [2006], McGill and Brown [2007], Dercole and Rinaldi [2008]). Some authors instead use $R_0(x,v,u)$ as the measure of fitness in this methodology (Roff [1992]).

If evolution is absent, $\theta^2 = 0$, then $u(t) = u_0$ for all t and the fundamental bifurcation theorem described in Section 2 applies to the population dynamic equation (13a). If $\theta^2 > 0$, a fundamental bifurcation theorem for the evolutionary model (13) is given in Cushing [2010] for the case when $P = P(x,v)$ and $r = r(x,v)$ do not depend on the mean trait u, which is the case in Section 3 in which we are interested.

An extinction equilibrium of the evolutionary model (13) is an equilibrium $(x,u) = (0,u)$. An extinction equilibrium occurs at and only at a *critical trait* $u = u^*$, i.e., a trait for which

$$\left.\frac{\partial r\,(0,v)}{\partial v}\right|_{v=u^*}=0. \tag{14}$$

With $r^*=r(0,u^*)$ as a bifurcation parameter, the local bifurcation of positive equilibria of (13) (i.e., equilibria (x,u) with $x\in R_+^2$) from an extinction equilibrium $(x,u)=(0,u^*)$ at $r^*=1$ (equivalently $R_0^*=1$) has been established in Cushing [2010]. If

$$\left.\frac{\partial^2 r\,(0,v)}{\partial v^2}\right|_{v=u^*}<0, \tag{15}$$

then the extinction equilibrium loses (local asymptotic) stability as r^* increases through 1 and the stability or instability of the bifurcating positive equilibria depends on the direction of bifurcation (as in the nonevolutionary model). The bifurcation is forward and stable if $\kappa^*>0$ and backward and unstable if $\kappa^*<0$ where

$$\kappa^*\triangleq -w_L^*\left(\nabla^* p_{ij}w_R^*\right)w_R^*,$$

and w_L^*,w_R^* are (positive) left and right eigenvectors in R_+^2 of $P(0,u^*)$ associated with eigenvalue $r^*=1$. Here, $\nabla^* p_{ij}$ denotes the (row vector) gradient of $p_{ij}(x)$ with respect to $x=\mathrm{col}(x_1,x_2)$ evaluated $(x,u)=(0,u^*)$ when $r^*=1$ (equivalently $R_0^*=1$). (If the inequality (15) is reversed, then both the extinction equilibrium and the bifurcating positive equilibria are unstable for r^* less than and greater than 1.)

We note in passing that the results in Cushing [2011] show that $R_0(0,v)$ can replace $r(0,v)$ in the critical trait equation (14) and in the local maximum criterion (15). This is often useful in applications since formulas for R_0 are often available when formulas for r are not.

When $r(0,v)$ (equivalently $R_0(0,v)$) has a local maximum at a critical trait $v=u^*$ when $r(0,u^*)=1$ ($R_0(0,u^*)=1$), one key ingredient for a strong Allee effect is available in the evolutionary model (13), namely, a backward bifurcation when $\kappa^*<0$. As in the nonevolutionary model, the occurrence of a strong Allee effect, in the presence of a backward bifurcation, requires the existence of another positive attractor. The *a priori* bound criterion A2 that guarantees the existence of at least one other positive equilibrium for the nonevolutionary model is not, as yet, available for the evolutionary model. This is because the existence of a global, unbounded bifurcating continuum of positive equilibria has not yet been established for the evolutionary model (13).

However, we show that a strong Allee effect can occur in the evolutionary model by means of numerical simulations of the evolutionary version of the specific model

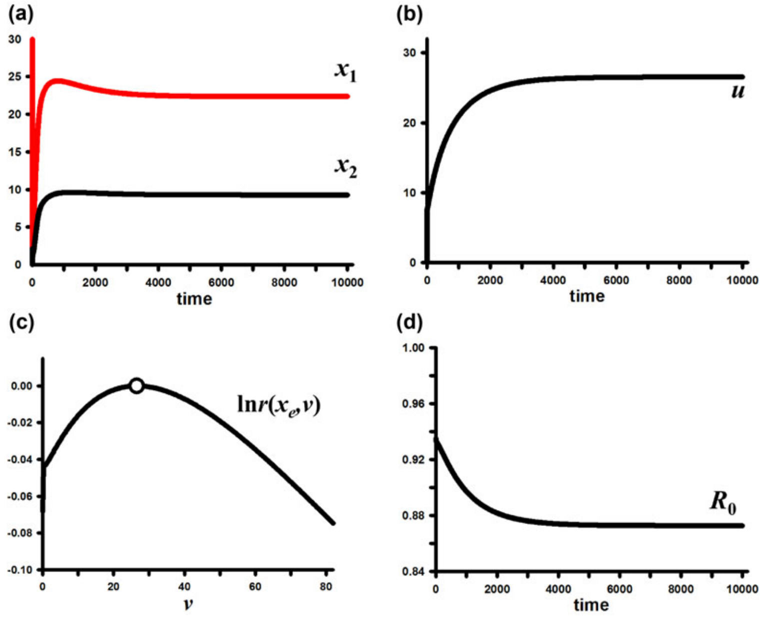

FIGURE 3. This simulation of (13) uses coefficients (6)–(11) and the same parameter values as in Figure 2b except that now the mean cannibalism intensity $u(t)$ is allowed to evolve from $u_0 = 0$ (a noncannibalistic state) with variance $\theta^2 = 10$. Simulations were computed for 10,000 time steps. (a) and (b) The population equilibrates to $(x_1, x_2) \approx (22.4, 9.29)$. The mean trait $u(t)$, initially equal to $u_0 = 0$ (a noncannibalistic population), initially increases rapidly before slowly (monotonically) equilibrating to $u = u_e \approx 26.5$ (a cannibalistic population). (c) This plot of the fitness landscape $\ln r(x_e, v)$ shows a global maximum as a function of $v > 0$ attained at $v = u_e$ (open circle). (d) $R_0(0, u(t))$ decreases from $R_0(0, 0) \approx 0.935$ to $R_0(0, u_e) \approx 0.873$, and hence remains less than 1.

considered in Section 3 based on the ingredients (6)–(11). We use the cannibalism efficiency parameter v as the evolving trait.

We use the parameter values in Figure 2b, which imply that the noncannibalistic population suffers extinction, because the resource ρ is so low that $r < 1$. In Figure 2c, we saw that by introducing cannibalism into the model, by choosing $v = 5$, the resulting cannibalistic population will not go extinct. In Figure 3, we see a different scenario, in which cannibalism is allowed to enter the population evolutionarily. Starting from the absence of cannibalism, $u_0 = 0$, we see in Figure 3 a sample orbit of the evolutionary version (13) of the model showing that the population adapts by increasing the (mean) cannibalism intensity $u(t)$ from 0 to an positive equilibrium level u_e (Figure 3b) and, in so doing, no longer suffers extinction (Figure 3a). Moreover, Figure 3c shows that the equilibrium mean trait u_e is located at a global maximum of the adaptive landscape $\ln r(x_e, v)$ (as a function of v) and therefore is an ESS (Vincent and Brown [2005], McGill and Brown [2007]). Figure 3d shows

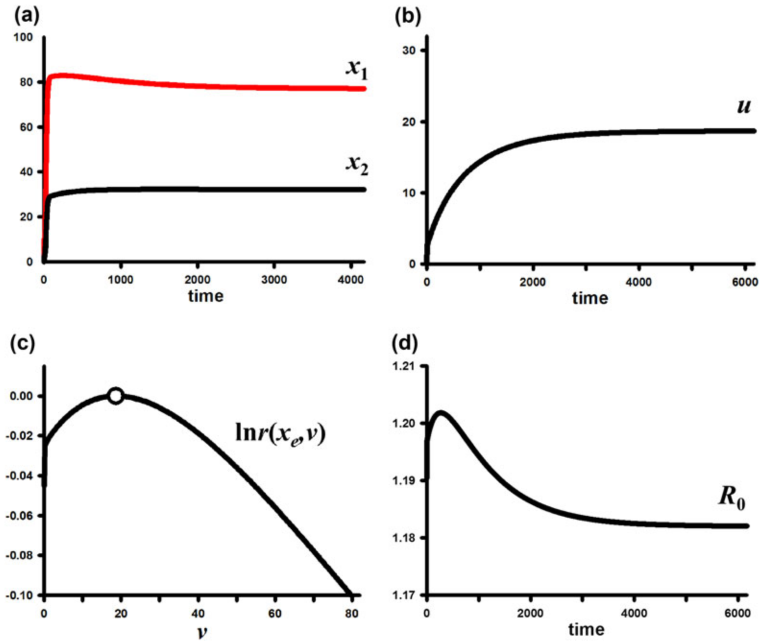

FIGURE 4. This simulation of (13) uses coefficients (6)–(11) and the same parameter values as in Figure 2a except that now the mean cannibalism intensity $u(t)$ is allowed to evolve from $u_0 = 0$ (a noncannibalistic state) with variance $\theta^2 = 10$. Simulations were computed for 10,000 time steps. (a) and (b) The population equilibrates to $(x_1, x_2) \approx (76.9, 32.2)$. The mean trait $u(t)$, initially equal to $u_0 = 0$ (a noncannibalistic population), initially increases rapidly before slowly (monotonically) equilibrating to $u_e \approx 18.7$ (a cannibalistic population). (c) This plot of the fitness landscape $\ln r(x_e, v)$ shows a global maximum as a function of $v > 0$ attained at $v = u_e$ (open circle). (d) $R_0(0, u(t))$ increases from $R_0(0,0) \approx 1.19$ to $R_0(0, u_e) \approx 1.18$, and hence remains greater than 1.

that the inherent net reproductive number $R_0(0, u(t))$ remains less than 1 (and in fact, decreases) during this entire evolutionary adaptation.

For the simulation in Figure 3, calculations show that there is a unique critical mean trait $u^* \approx 4.20$ (obtained by numerically solving (14)); that

$$\left.\frac{\partial^2 r(0,v)}{\partial v^2}\right|_{v=u^*} \approx -1.28 \times 10^{-4},$$

and hence (15) holds; and that $\kappa^* \approx -0.574 < 0$ and hence a backward bifurcation occurs. Changing the initial condition $(x_1, x_2) = (10, 0)$ to a small value of x_1 results in population extinction (not shown in Figure 3).

Figure 4 shows the changes that occur when the resource level ρ is increased to the level in Figure 2a when the noncannibalistic population does not go extinct because $R_0 > 1$. In the evolutionary case shown in Figure 4, the noncannibalistic population still adapts by introducing cannibalism, albeit at a lower ESS level (Figure 4b) than in the adverse environment (Figure 3b). In this case, $R_0(0, u(t))$ remains (and equilibrates) higher than 1 during the approach to equilibrium.

5. Concluding remarks. Motivated by an example from colonial seabirds in which depressed resources are associated with increased egg cannibalism, we have constructed a low dimensional, proof-of-concept, two-stage population model in which adults cannibalize juveniles and the vital rates, including the cannibalism rate, depend on the (noncannibalism) food resource availability. The model includes positive effects of cannibalism on adult survivorship and negative effects of cannibalism on juvenile survivorship. We also constructed an evolutionary version of this model in which a parameter that measures cannibalism aggressiveness is allowed to evolve.

In our model, increased (noncannibalism food) resource levels ρ have a positive effect on fecundity and survivorship and a negative effect on the adult cannibalism rate. We showed that in the absence of cannibalism, the population model has a forward bifurcation of stable positive equilibria at $R_0(\rho) = 1$, so that when resources are high ($R_0(\rho) > 1$), the population survives, but when resources are low ($R_0(\rho) < 1$), the population goes extinct. If adult cannibalism is present and its benefit to adult survival is sufficiently high, then the bifurcation can be backward and the bifurcating branch of equilibria, unstable near the bifurcation point, can turn back to the right at a saddle-node bifurcation, and become stable. Therefore, the benefit of cannibalism for adult survival can cause a strong Allee effect, that is, a range of $R_0(\rho)$ values less than one over which there are two attractors: the extinction state and a positive stable equilibrium. This indicates that adult cannibalism on juveniles can allow a population to avoid extinction during when the availability of environmental food resource is so low (caused, perhaps, by climate or other environmental changes) that the population is threatened with extinction.

In the evolutionary model, the cannibalism efficiency of an individual adult is subject to change by means of Darwinian evolution. This model predicts, in circumstances when availability of environmental food resource and the benefits for adult survival by cannibalism are so low that the population will go extinct, that it is possible for evolution to raise the mean level of cannibalism efficiency among the adults to a level at which the population will not go extinct. Moreover, the mean level of cannibalism efficiency attained is an evolutionary stable strategy. Interestingly, should the resource availability increase to a level at which the population will not go extinct even in the absence of adult cannibalism (due, say, to a recovery of environmental factors), the model predicts that the mean cannibalism efficiency will not evolve to 0.

The proof-of-concept model used in this study, although not descriptive of a particular ecological system, shows that adult cannibalism on juveniles can be beneficial to the survival of the population and can serve as an ESS trait. In future studies of the colonial seabird system in relation to local sea surface temperature, we will derive and analyze models that incorporate more detailed and realistic mechanisms of cannibalism, as well as other life history characteristics that are affected by climate change.

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