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Population Dynamics in a Microfounded Predator-PreyModel

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Population Dynamics in a Microfounded Predator-Prey Model

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Population Dynamics in a Microfounded Predator-Prey Model

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Abstract. This paper analyzes the dynamics of a two-dimensional microfounded predator-prey model. It is shown that the dynamics closely resemble those of a model commonly used in mathematical biology if parameters of the latter are suitably restricted. The positive equilibrium of the microfounded model is globally asymptotically stable for positive initial values largely irrespective of the parameter values chosen. If a version of Allee's Law is included, however, species extinction becomes possible.

Keywords: population dynamics; ratio dependence; species extinction

JEL-Classification: Q20

1 Introduction

Mathematical biologists have recently extensively studied an alternative to the classical Lotka-Volterra model and its variations. The classical approach has been losing ground since some of its predictions are not in line with many field observations. The alternative theory relies on the so-called ratio-dependent predator-prey models.[1] Kuang and Beretta (1998) have analyzed the global dynamic behavior of the following two-dimensional ratio-dependent type predator-prey model:

$$\dot{n}_1 = n_1 \left[a\left(1 - \frac{n_1}{K}\right) - \frac{b n_2}{n_1 + m n_2} \right], \tag{1}$$

$$\dot{n}_2 = n_2 \left[\frac{f n_1}{n_1 + m n_2} - d \right]. \tag{2}$$

Here, n_1 and n_2 denote the prey and the predator population, respectively, and a, b, d, f, m, and K are positive parameters whose biological interpretation can be found in Kuang and Beretta (1998), e.g. These authors have shown that the system possesses a unique and globally asymptotically stable positive equilibrium (that is, an equilibrium where both n_1 and n_2 are positive) for positive initial values if $f > d$ and $am \geqq b$. While $f > d$ is a necessary condition for the existence of such an equilibrium, the condition $am \geqq b$ is sufficient for its global stability but not necessary for existence. If $am < b$, the global dynamic behavior of the model changes substantially. E.g., extinction of both species becomes possible. A further analysis of these equations can be found in Hsu et al. (2001), where it is shown that even limit cycles and heteroclinic cycles may exist if $am < b$.

[1] It should be noted that the debate on the appropriate type of models is not yet finished and that the ratio-dependent models do also have their critics, cf. e.g. Abrams and Ginzburg (2000) and Deng et al. (2003).

A common feature of conventional predator-prey models is that they are macro approaches in the sense that populations and their development in time are the basic units of analysis. As Eichner and Pethig (2004a) put it, these macro approaches neglect the processes at the micro level of preying and being preyed upon which ultimately generate the growth functions describing the population dynamics. Such a microfoundation of predator-prey models based on economic methodology has been initiated by Hannon (1976) and further developed by Tschirhart (2000), Pethig and Tschirhart (2001), and Eichner and Pethig (2004b), e.g.

The present paper focuses on the following microfounded two-dimensional system introduced by Eichner and Pethig (2004b):

$$\dot{n}_1 = n_1 \left[A^1(n_1) \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\bar{z}_1 \frac{(1-\alpha_1)[n_1 e_1 + n_2 e_2]}{(1-\alpha_1)[n_1 e_1 + n_2 e_2] + \alpha_1 n_2 e_2} \right)^{1-\alpha_1} - \gamma_1 \right], \tag{3}$$

$$\dot{n}_2 = n_2 \left[A^2(n_2) \bar{z}_2^{1-\alpha_2} \left(\frac{n_1 \alpha_1 \bar{z}_1}{n_2} \frac{n_2 e_2}{n_2 e_2 + (1-\alpha_1) n_1 e_1} \right)^{\alpha_2} - \gamma_2 \right]. \tag{4}$$

For $i = 1,2$, e_i, γ_i, $\tilde{n}_i$ and $\bar{z}_i$ as well as r_0 are positive constants, respectively, while $0 < \alpha_i < 1$. Cf. Eichner and Pethig (2004b) for the ecological or economic interpretation of these parameters. The functions A^i are defined by

$$A^i(n_i) := \min \left\{ 1, \frac{n_i}{\tilde{n}_i} \right\}, \quad i = 1,2. \tag{5}$$

The inclusion of the functions A^i corresponds to the idea that the organism's generation of net offspring is the more hampered, the further n_i drops below some critical population level $\tilde{n}_i > 0$. According to Allee's Law, species i may be called an endangered species if $n_i < \tilde{n}_i$ (cf. Berryman, 2003).

Regarding the microfoundation, equations (3) and (4) are derived in Eichner and Pethig (2004b) from the maximization of a net-offspring function

$$B^i(x_{i-1}, z_i, n_i) = A^i(n_i) x_{i-1}^{\alpha_i} (\bar{z}_i - z_i)^{1-\alpha_i} - \gamma_i, \quad i = 1,2,$$

of the representative organism of species i, where $0 < \alpha_i < 1$ and $\gamma_i > 0$, subject to the resource constraint

$$e_i + p_i z_i \geqq p_{i-1} x_{i-1}, \quad i = 1,2.$$

x_{i-1} is organism i's intake of biomass of its prey species $i-1$ and z_i is organism i's loss of own biomass to its predator, species $i+1$. For $i = 1$, $x_{i-1} = x_0$ is the demand of organism 1 for a basic resource whose total supply per period is $r_0 > 0$. $e_i > 0$ is some exogenous lump-sum *income* of species i and p_i is the *market price* of biomass of species i. Since species 2 is the top predator its biomass price is set $p_2 \equiv 0$. The equilibrium conditions

$$r_0 = n_1 x_0, \quad n_1 z_1 = n_2 x_1$$

are used to determine the equilibrium values of p_0, p_1, x_0, x_1, and z_1, which are substituted into the net-offspring functions. Equations (3) and (4) then follow by substitution into the dynamic equations $\dot{n}_i = B^i n_i$, $i = 1,2$.

Eichner and Pethig (2004b) have analyzed the resulting dynamics of a three-dimensional food chain by means of numerical simulations. Among their results is that the positive equilibrium, which they have shown to be unique, is approached for all positive initial values if one sets $A^i(n_i) \equiv 1,\ i = 1,2,3$. Thus, extinction in the three-dimensional system seems to be impossible unless Allee's Law is explicitly considered. The purpose of the present paper is to give a complete characterization of the dynamics in case of a two-dimensional system with just two species.

As a slight generalization of the two-dimensional case, the parameters $1-\alpha_i$ are replaced by $\beta_i \geqq 0$ and the restrictions $0 < \alpha_i < 1$ by $\alpha_i > 0$. Repeating the derivations of Eichner and Pethig (2004b) for the two species case yields the differential equations

$$\dot{n}_1 = n_1 \left[A^1(n_1) \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\bar{z}_1 \frac{\beta_1 [n_1 e_1 + n_2 e_2]}{\beta_1 [n_1 e_1 + n_2 e_2] + \alpha_1 n_2 e_2} \right)^{\beta_1} - \gamma_1 \right],$$

$$\dot{n}_2 = n_2 \left[A^2(n_2) \bar{z}_2^{\beta_2} \left(\frac{n_1 \alpha_1 \bar{z}_1}{n_2} \frac{n_2 e_2}{\beta_1 [n_1 e_1 + n_2 e_2] + \alpha_1 n_2 e_2} \right)^{\alpha_2} - \gamma_2 \right].$$

As $\bar{z}_2^{\beta_2}$ is just a constant in the two-dimensional setting, it will be assumed that $\beta_2 = 0$. This assumption simplifies the analysis without substantially altering the results ($\beta_2 > 0$ would merely necessitate a modification of some parameter assumptions). In this case, the differential equations can be given a slightly simpler appearance:

$$\dot{n}_1 = n_1 \left[A^1(n_1) \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\bar{z}_1 \frac{\beta_1 [n_1 e_1 + n_2 e_2]}{\beta_1 [n_1 e_1 + n_2 e_2] + \alpha_1 n_2 e_2} \right)^{\beta_1} - \gamma_1 \right], \tag{6}$$

$$\dot{n}_2 = n_2 \left[A^2(n_2) \left(\frac{n_1 \alpha_1 \bar{z}_1 e_2}{\beta_1 [n_1 e_1 + n_2 e_2] + \alpha_1 n_2 e_2} \right)^{\alpha_2} - \gamma_2 \right]. \tag{7}$$

A further simplification follows by setting $A^i(n_i) \equiv 1,\ i = 1,2$, for the time being. Letting

$$m := \frac{\alpha_1 + \beta_1}{\beta_1} \frac{e_2}{e_1}, \quad f := \frac{\alpha_1 e_2}{\beta_1}, \quad c := \frac{\bar{z}_1}{e_1},$$

equations (6) and (7) take the form

$$\dot{n}_1 = n_1 \left[\left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1} - \gamma_1 \right], \tag{8}$$

$$\dot{n}_2 = n_2 \left[\left(\frac{f c n_1}{n_1 + m n_2} \right)^{\alpha_2} - \gamma_2 \right]. \tag{9}$$

While equation (9) is now qualitatively equivalent to (2) if $\alpha_2 = 1$, equation (8) cannot be transformed into equation (1) using the present setting. Eichner and Pethig (2004a) have shown, however, that equation (1) can be derived from a slightly modified micro model of the ecosystem.

The remainder of this paper is devoted to an analysis of equations (6) and (7). An interesting question is whether the dynamic properties of these equations are similar to those of equations (1) and (2). To answer this question, Section 2 starts with an analysis of the simplified equations (8) and (9). The results will then be

used to consider the original equations (6) and (7) in Section 3. Section 4 provides a concluding comparison of the microfounded and the conventional model. It will be shown that the dynamics of (8) and (9) if $fc > \gamma_2^{1/\alpha_2}$ and $0 < \alpha_1 < 1$ closely resemble those of (1) and (2) if $f > d$ and $am \geqq b$. While according to (1) and (2) extinction is possible if $f > d$ and $am < b$, extinction in the microfounded model is impossible under reasonable assumptions unless Allee's Law is included, that is, unless equations (6) and (7) instead of (8) and (9) are used.

2 Analysis of Equations (8) and (9)

2.1 Equilibria and Local Stability

As the right-hand sides of (8) and (9) are not defined at $(n_1, n_2) = (0,0)$, it will be assumed that $\dot{n}_1 = \dot{n}_2 = 0$ if $n_1 = n_2 = 0$ by definition. Calculating the limit for $\lim_{(n_1,n_2)\to(0,0)}$ shows that under this assumption both $\dot{n}_1$ and $\dot{n}_2$ are continuous on $R_+^2 = \{(n_1, n_2) \in R^2 : n_1 \geqq 0, n_2 \geqq 0\}$ if $0 < \alpha_1 < 1$, although not differentiable at $(0,0)$, cf. Appendix A. A similar argument applies with respect to equations (6) and (7).

All assumptions supposed to hold in the sequel are summarized as follows. They will not be repeated each time a proposition is stated.

Assumptions. *All parameters appearing in equations (8) and (9) [as well as in (6) and (7)] are positive. In addition,*

$$0 < \alpha_1 < 1, \quad 0 < \alpha_2 \leqq 1, \quad \textit{and} \quad fc > \gamma_2^{1/\alpha_2}.$$

The initial values of n_1 and n_2 are non-negative. If $n_1 = n_2 = 0$, then $\dot{n}_1 = \dot{n}_2 = 0$.

These assumptions serve the following purposes: $0 < \alpha_1 < 1$ ensures continuity of (8) and (9) on R_+^2, $fc > \gamma_2^{1/\alpha_2}$ is necessary for the existence of a positive equilibrium, and $0 < \alpha_2 \leqq 1$ will be needed when analyzing equation (7).

There are three equilibria. To begin with, set $n_1 = 0$ and $n_2 > 0$, implying $\dot{n}_1 = 0$ and $\dot{n}_2 = -\gamma_2 n_2$. Thus, there is a first (trivial) equilibrium $E_0 = (0,0)$ and there can be no other equilibrium where $n_1 = 0$. It is obvious that $(0,0)$ is stable along the n_2-axis. Thus, if there is no prey, the predator will become extinct.

Setting $n_2 = 0$ and $n_1 > 0$ implies $\dot{n}_2 = 0$ and

$$\dot{n}_1 = r_0^{\alpha_1} \bar{z}_1^{\beta_1} n_1^{1-\alpha_1} - \gamma_1 n_1.$$

It is straightforward that there is a second equilibrium E_1 at

$$(n_1, n_2) = \left(r_0 \frac{\bar{z}_1^{\beta_1/\alpha_1}}{\gamma_1^{1/\alpha_1}}, 0 \right)$$

that is stable along the n_1-axis. Thus, if there is no predator, the prey population reaches a steady state that is directly proportional to the size of the basic resource, r_0.

A third equilibrium, E_2, entails positive populations of both species. If $n_1 > 0$ and $n_2 > 0$, setting $\dot{n}_2 = 0$ yields

$$n_2 = \underbrace{\frac{fc - \gamma_2^{1/\alpha_2}}{m\gamma_2^{1/\alpha_2}}}_{=:q} n_1 = q n_1. \tag{10}$$

Hence, a positive equilibrium cannot exist unless the condition

$$fc > \gamma_2^{1/\alpha_2} \tag{11}$$

holds, which has already been assumed. Since γ_2^{1/α_2} should usually be a small number in relation to fc, this assumption is rather natural. Upon subsitution of (10) into $\dot{n}_1 = 0$ one gets

$$n_1 = \frac{r_0}{\gamma_1^{1/\alpha_1}} \left(\frac{c(e_1 + qe_2)}{1 + mq} \right)^{\beta_1/\alpha_1},$$

which together with (10) describes the positive equilibrium E_2. Observe that in any of the three equilibria thus considered the population of both species is proportional to the size of the basic resource, r_0.

As for the stability of the positive steady state, the Jacobian of system (8), (9) evaluated at E_2 can be shown to have the following pattern of signs (cf. Appendix B):

$$\operatorname{sgn}(J) = \operatorname{sgn} \begin{pmatrix} \partial \dot{n}_1/\partial n_1 & \partial \dot{n}_1/\partial n_2 \\ \partial \dot{n}_2/\partial n_1 & \partial \dot{n}_2/\partial n_2 \end{pmatrix} = \begin{pmatrix} - & - \\ + & - \end{pmatrix} \tag{12}$$

Therefore, $\operatorname{Tr}(J) < 0$ and $|J| > 0$, implying that the equilibrium E_2 is locally asymptotically stable by the Routh-Hurwitz criterion.

These results are summarized in

Proposition 1 *There are three equilibria.* $E_0 = (0,0)$ *is locally asymptotically stable along the* n_2*-axis,* $E_1 = (r_0 \bar{z}_1^{\beta_1/\alpha_1}/\gamma_1^{1/\alpha_1}, 0)$ *is locally asymptotically stable along the* n_1*-axis, and*

$$E_2 = \left(\frac{r_0}{\gamma_1^{1/\alpha_1}} \left(\frac{c(e_1 + qe_2)}{1 + mq} \right)^{\beta_1/\alpha_1}, q \frac{r_0}{\gamma_1^{1/\alpha_1}} \left(\frac{c(e_1 + qe_2)}{1 + mq} \right)^{\beta_1/\alpha_1} \right)$$

is locally asymptotically stable.

2.2 Global Stability

The global dynamic behavior of solutions can be determined using the phase diagram 1, whose derivation is as follows. From (10), the isocline $\dot{n}_2 = 0$ is a positively sloped straight line through the origin (unionized with the n_1-axis) in (n_1, n_2)-space if conditon (11) holds. Setting $\dot{n}_1 = 0$ and solving for n_2 yields the following expression (unionized with the n_2-axis) for the isocline $\dot{n}_1 = 0$:

$$n_2 = \frac{\beta_1 e_1 n_1 \left[\bar{z}_1 - \gamma_1^{1/\beta_1} (n_1/r_0)^{\alpha_1/\beta_1} \right]}{e_2(\alpha_1 + \beta_1)\gamma_1^{1/\beta_1} (n_1/r_0)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_2}. \tag{13}$$

Considering the denominator, it is straightforward that

$$\text{denominator} \gtreqless 0 \iff n_1 \gtreqless r_0 \left(\frac{\beta_1}{\alpha_1 + \beta_1} \bar{z}_1 \right)^{\beta_1/\alpha_1} \frac{1}{\gamma_1^{1/\alpha_1}} =: \underline{n}_1. \tag{14}$$

Thus, there is a vertical asymptote at $\underline{n}_1$. Similarly, under the precondition that $n_1 > 0$,

$$\text{numerator} \gtreqless 0 \iff n_1 \lesseqgtr r_0 \bar{z}_1^{\beta_1/\alpha_1} \frac{1}{\gamma_1^{1/\alpha_1}} =: \overline{n}_1. \tag{15}$$

Therefore, the isocline cuts the n_1-axis at the equilibrium E_1 where $n_1 = \overline{n}_1 > \underline{n}_1$ (and at the equilibrium E_0, where $n_1 = 0$). Comparing the sign patterns of the numerator and the denominator shows that the isocline lies below the n_1-axis for $0 < n_1 < \underline{n}_1$ and $n_1 > \overline{n}_1$, while it lies above the axis if $\underline{n}_1 < n_1 < \overline{n}_1$.

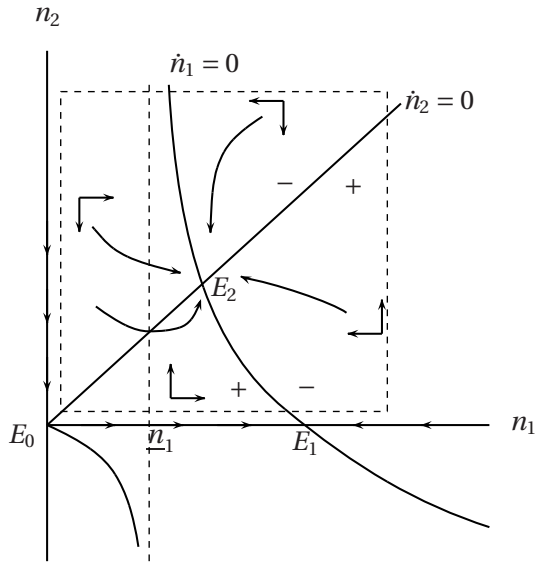

Figure 1. Phase Diagram of Equations (8), (9)

As has been shown in Appendix B, the cross partial derivatives of (8) and (9) are

$$\frac{\partial \dot{n}_1}{\partial n_2} < 0 \quad \text{and} \quad \frac{\partial \dot{n}_2}{\partial n_1} > 0,$$

respectively. These partial derivatives give rise to the + and − signs indicating the directions of motion off the zero isoclines.[2] Putting all this information together yields the phase diagram 1. For the sake of completeness, it is shown in Appendix C that the slope of the isocline $\dot{n}_1 = 0$ is negative if $\underline{n}_1 < n_1 < \overline{n}_1$.

[2] Due to the existence of the vertical asymptote, there is one specialty to be taken care of. Above but near the isocline $\dot{n}_1 = 0$ in the region where n_2 is negative, $\dot{n}_1 < 0$. As $\dot{n}_1 > 0$ below $\dot{n}_1 = 0$ in the positive region, the question arises where the sign of $\dot{n}_1$ changes. Inspection of equation (8) shows that a sign change off the isocline $\dot{n}_1 = 0$ derived from (13) (or from $n_1 = 0$) is possible only if (8) has a vertical asymptote at $n_1 + m n_2 = 0$. Thus, if $n_1 > 0$ the sign change must occur in the irrelevant region where $n_2 < 0$.

The phase diagram reveals that the equilibrium E_2 is globally asymptotically stable for strictly positive initial values. The proof relies on the fact that it is always possible to draw a rectangular closed region from which the trajectories cannot escape (cf. the dashed rectangle in Figur 1). This proves that the differential equations (8) and (9) have a solution defined for all $t \geqq 0$ (Hirsch and Smale, 1974, p. 172). According to the Generalized Poincaré-Bendixson Theorem (cf. Perko, 1996, p. 243), any limit point of trajectories must be an equilibrium if there exists neither a closed orbit nor a separatrix cycle. As the considered region contains just one equilibrium which is locally asymptotically stable, there is no separatrix cycle. Closed orbits are ruled out by the direction of movements in the four regions separated by the zero-isoclines, or, more rigorously, by Dulac's criterion (cf. Appendix D). It follows that there is just one possible limit point of trajectories if $t \to \infty$, the equilibrium E_2. This proves global stability.

Notice that Figure 1 gives a qualitatively complete picture of the dynamics of system (8), (9). If both initial values are positive, the equilibrium E_2 will be reached and both species will survive. If the intial value of the predator species is zero, a positive inital population of the prey species will reach the equilibrium E_1. Finally, if the initial value of the prey species is zero, E_0 will be reached and the predator species becomes extinct. The analysis is summarized in

Proposition 2 *Each trajectory of system (8), (9) converges to an equilibrium. If* $n_1(0) = 0 < n_2(0)$, $\lim_{t\to\infty}(n_1(t), n_2(t)) = E_0$. *If* $n_1(0) > 0 = n_2(0)$, $\lim_{t\to\infty}(n_1(t), n_2(t)) = E_1$. *If* $n_1(0) > 0$ *and* $n_2(0) > 0$, $\lim_{t\to\infty}(n_1(t), n_2(t)) = E_2$.

3 Analysis of Equations (6) and (7)

3.1 Partitioning the Phase Diagram

Using similar parameters as in equations (8) and (9), equations (6) and (7) read

$$\dot{n}_1 = n_1 \left[A^1(n_1) \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1} - \gamma_1 \right], \tag{6'}$$

$$\dot{n}_2 = n_2 \left[A^2(n_2) \left(\frac{f c n_1}{n_1 + m n_2} \right)^{\alpha_2} - \gamma_2 \right], \tag{7'}$$

where $A^i(n_i)$ as defined in (5) is repeated here for convenience:

$$A^i(n_i) := \min \left\{ 1, \frac{n_i}{\tilde{n}_i} \right\}, \quad i = 1, 2.$$

As a first step, observe that the phase diagram can now be partitioned into three regions depending on the values of $\tilde{n}_i$. As long as $n_i \geqq \tilde{n}_i$, the phase diagram 1 applies as before. For the vector field generated by (8) and (9) always points inwards any closed rectangular region lying in the positive quadrant, cf. Figure 1. If $n_i < \tilde{n}_i$ for $i = 1$ and/or $i = 2$, the dynamics will change. The result will depend on the relative position of the equilibrium E_2. Figure 2 indicates the situation for the case where the equilibrium values of n_1 and n_2 both exceed $\tilde{n}_1$ and $\tilde{n}_2$, respectively.

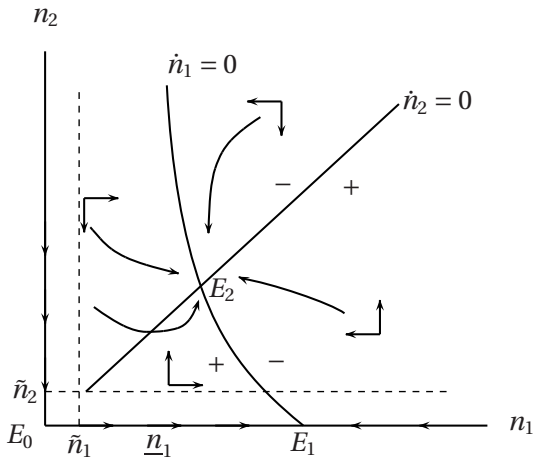

Figure 2. Partitioning the Phase Diagram

It remains to determine the shape of the isoclines in the regions to the left of $\tilde{n}_1$ and below $\tilde{n}_2$.

As there are a lot of feasible parameter configurations giving rise to various details of the implied dynamics, this section solely relies on the analysis of representative phase diagrams without analytically analyzing local stability or instability of equilibria, which is straightforward in most cases, however. Similarly, the exclusion of closed orbits is not explicitely considered as the phase diagrams reveal that trajectories are always trapped in either the basin of attraction of the positive equilibrium or in a region where at least one species eventually becomes extinct.

3.2 Small Predator Population

Below $\tilde{n}_2$, the shape of the isocline $\dot{n}_1 = 0$ is left unchanged, while $\dot{n}_2 = 0$ can be solved for n_1 to yield

$$n_1 = \frac{(\gamma_2 \tilde{n}_2)^{1/\alpha_2} m n_2}{f c n_2^{1/\alpha_2} - (\gamma_2 \tilde{n}_2)^{1/\alpha_2}}, \tag{16}$$

which is positive at $n_2 = \tilde{n}_2$ due to (11). At $n_2^a := \gamma_2 \tilde{n}_2 / (f c)^{\alpha_2} < \tilde{n}_2$, there is a horizontal asymptote. As n_2 declines further, n_1 in (16) becomes negative. In addition, it is shown in Appendix E that $\alpha_2 \leqq 1$ is a sufficient condition for the slope to be negative. Thus, the relevant part of the isocline has the shape shown in Figure 3.

There emerges a new equilibrium E_3, which is unstable, however. As the direction arrows indicate, the equilibrium E_2 may even be approached if $n_2 < \tilde{n}_2$, that is, if the predator is an endangered species. Extinction of the endangered species is certain, however, if $n_2 \leqq n_2^a$. The system then approaches the equilibrium E_1 on the n_1-axis, where only the prey survives.

Regarding the policy implications of the complete model of Eichner and Pethig (2004b), it should be noted that humans may influence the ecosystem by variation of the size of the basic resource, r_0. While the isocline $\dot{n}_2 = 0$ is independent of r_0, $\dot{n}_1 = 0$ will shift to the left as r_0 decreases. It is therefore interesting to analyze the behavior of the system as E_2 vanishes sliding along $\dot{n}_2 = 0$ when r_0 decreases. Such

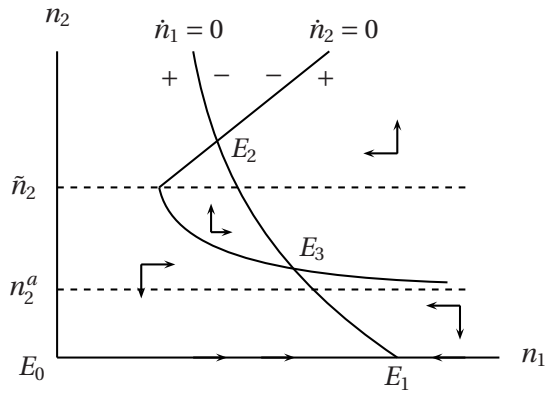

Figure 3. Dynamics in Case of $n_2 < \tilde{n}_2$

a case, where the equilibrium E_2 does not exist as it would involve an equilibrium value of n_2 which is smaller than $\tilde{n}_2$, is shown in Figure 4. As the direction arrows indicate, the equilibrium E_1 will be approached. Notice, however, that this result presupposes that $n_1 \geqq \tilde{n}_1$, as the modifications of the dynamic system arising if $n_1 < \tilde{n}_1$ have not been taken into account yet.

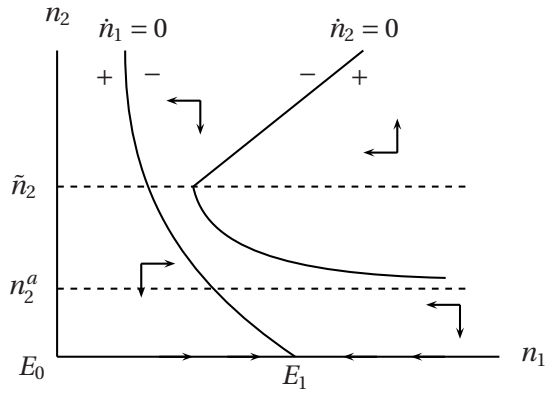

Figure 4. Dynamics in Case of $n_2 < \tilde{n}_2$ if E_2 Vanishes

3.3 Small Prey Population

To the left of $\tilde{n}_1$, the shape of the isocline $\dot{n}_2 = 0$ is left unchanged, while $\dot{n}_1 = 0$ from (6') can be solved for n_2 to yield

$$n_2 = \frac{\beta_1 e_1 n_1 \left[\bar{z}_1 n_1^{1/\beta_1} - (\gamma_1 \tilde{n}_1)^{1/\beta_1} (n_1/r_0)^{\alpha_1/\beta_1}\right]}{e_2(\alpha_1+\beta_1)(\gamma_1\tilde{n}_1)^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_2 n_1^{1/\beta_1}}. \tag{17}$$

Recall that $0 < \alpha_1 < 1$ and $\beta_1 > 0$. As to the denominator, it is straightforward that

$$\text{denominator} \gtreqless 0 \iff n_1 \lesseqgtr r_0^{\alpha_1/(\alpha_1-1)} \left(\frac{\beta_1}{\alpha_1+\beta_1}\bar{z}_1\right)^{\beta_1/(\alpha_1-1)} \frac{1}{(\gamma_1\tilde{n}_1)^{1/(\alpha_1-1)}} =: n_1^a. \tag{18}$$

Thus, there is a vertical asymptote at n_1^a. Similarly,

$$\text{numerator} \gtreqless 0 \iff n_1 \gtreqless r_0^{\alpha_1/(\alpha_1-1)} \bar{z}_1^{\beta_1/(\alpha_1-1)} \frac{1}{(\gamma_1 \tilde{n}_1)^{1/(\alpha_1-1)}} =: n_1^0. \tag{19}$$

Thus, the isocline cuts the n_1-axis at $n_1^0 < n_1^a$. Similar considerations as in Section 2.2 lead to the graph of the isocline shown in Figure 5. As to the + and − signs beneath the isocline, the remarks given in Footnote 2 apply analogously.

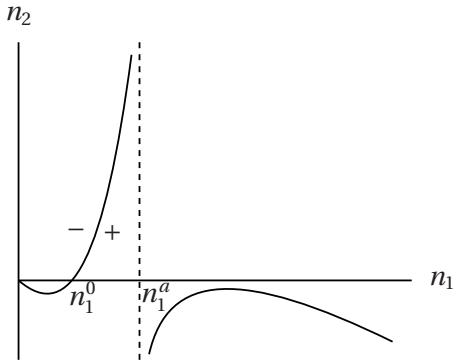

Figure 5. The Isocline $\dot{n}_1 = 0$ if $n_1 < \tilde{n}_1$

With respect to the dynamics, it is important whether a part of the isocline (17) in the positive region lies to the left of $\tilde{n}_1$. Setting $n_1^0 \gtreqless \tilde{n}_1$ shows that this condition is equivalent to $\tilde{n}_1 \gtreqless \overline{n}_1$:

$$n_1^0 \gtreqless \tilde{n}_1 \quad \iff \quad \tilde{n}_1 \gtreqless \overline{n}_1.$$

Thus, if $\tilde{n}_1 < \overline{n}_1$, there is a part of (17) for $n_1 > n_1^0$ lying to the left of $\tilde{n}_1$. Similarly, setting $n_1^a \gtreqless \tilde{n}_1$ yields

$$n_1^a \gtreqless \tilde{n}_1 \quad \iff \quad \tilde{n}_1 \gtreqless \underline{n}_1.$$

Therefore, the vertical asymptote of (17) lies to the left of $\tilde{n}_1$ if and only if $\tilde{n}_1$ lies to the left of the asymptote at $\underline{n}_1$ of equation (13). Proceeding under the reasonable assumption that $\tilde{n}_1 < \overline{n}_1$, it follows that two cases must be considered.

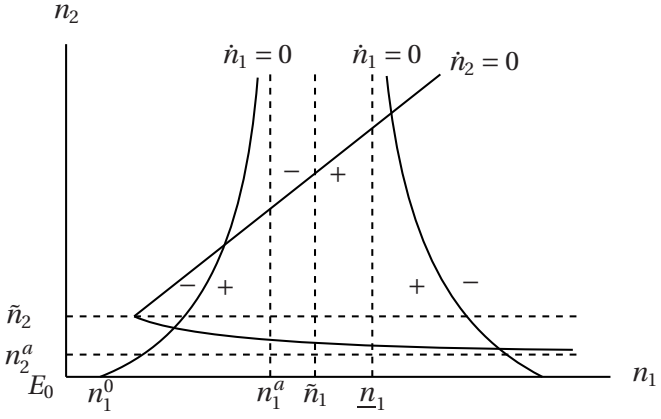

Figure 6. Dynamics in Case of $n_1 < \tilde{n}_1$ if $\tilde{n}_1 \leqq \underline{n}_1$

First, assume that $\tilde{n}_1 \leqq \underline{n}_1$. Figure 6 shows a possible configuration in this case. Other configurations are possible, depending on the relative position of $\tilde{n}_1$. In case of Figure 6, the predator will become extinct if the initial values of n_1 and n_2 are such that the system starts below the isocline $\dot{n}_2 = 0$ or sufficiently far to the left of the $\dot{n}_1 = 0$ isocline. Even the prey may become extinct as the equilibrium at $n_1 = n_1^0$ is unstable.

Second, let $\underline{n}_1 < \tilde{n}_1 < \overline{n}_1$. This implies that the right-hand part and the left-hand part of $\dot{n}_1 = 0$ are both valid only up to the point where $n_1 = \tilde{n}_1$. Moreover, as (6') is continuous at $n_1 = \tilde{n}_1$, the isocline itself is continuous here. One possible configuration is shown in Figure 7, where the positive equilibrium E_2 vanishes. Depending on parameter values, this equilibrium could as well persist. In case of Figure 7, the predator cannot survive in the long run.

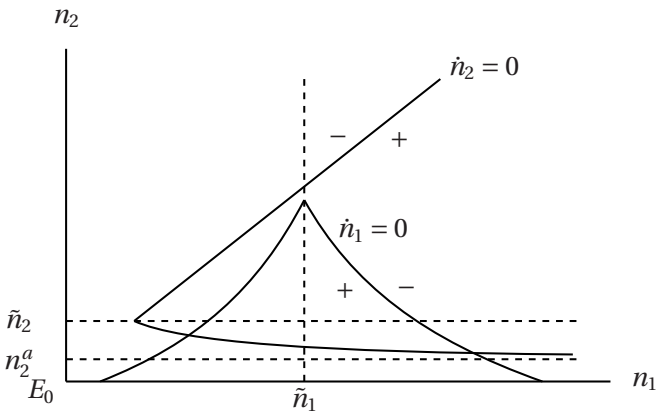

Figure 7. Dynamics in Case of $n_1 < \tilde{n}_1$ if $\underline{n}_1 < \tilde{n}_1 < \overline{n}_1$

Putting all information together yields the overall phase diagram, whose appearance depends on the specific values of $\tilde{n}_1$ and $\tilde{n}_2$. Figure 8 provides one example.

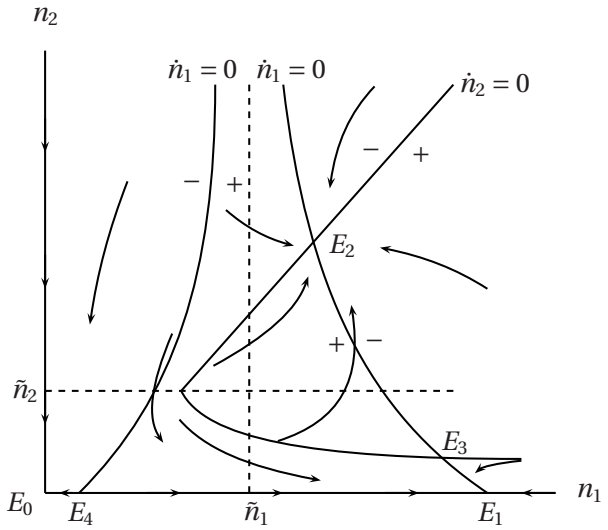

Figure 8. A Complete Phase Diagram

Although not all possible configurations have been analyzed in detail in this section, it is straightforward to consider the principle possibilities in terms of further phase diagrams. As with the examples given here, it is fairly obvious that the only possible limit points for $t \to \infty$ are equilibria. Exact proofs could be given along the lines in Section 2.2. The following proposition summarizes the main results.

Proposition 3 *Let* $(0,0) < (\tilde{n}_1, \tilde{n}_2) < E_2$. *Then each trajectory of system (6) and (7) converges to an equilibrium. The positive equilibrium* E_2 *is asymptotically stable and its basin of attraction covers at least* $\{(n_1, n_2) \in R^2 \mid n_1 \geqq \tilde{n}_1,\ n_2 \geqq \tilde{n}_2\}$. *There exist initial values* $n_1 \in (0, \tilde{n}_1)$ *and* $n_2 \in (0, \tilde{n}_2)$, *respectively, such that the predator or both species eventually become extinct.*

4 Discussion

If the functions $A^i(n_i)$ are set $A^i(n_i) \equiv 1$, the dynamics implied by equations (8) and (9) under conditions $fc > \gamma_2^{1/\alpha_2}$ and $0 < \alpha_1 < 1$ widely resemble the dynamics of the conventional model (1) and (2) if $f > d$ and $am \geqq b$, although the differential equations themselves are rather distinct. In both cases, there is a unique and globally stable equilibrium where both species survive if both initial values are positive. If there is no prey, the predator becomes extinct, and if there is no predator, the prey reaches a positive equilibrium. In fact, the phase diagram of (1) and (2) can be shown to look exactly like Figure 1 if $f > d$ and $am > b$. Empirically, it would be impossible to distinguish whether a given set of observations was generated by model (1) and (2) or by (8) and (9). If $f > d$ and $am = b$, the isocline $\dot{n}_1 = 0$ becomes a straight line, leaving the qualitative implications unchanged, however.

The condition $fc > \gamma_2^{1/\alpha_2}$ is necessary and (given other assumptions about parameters following from the micro approach) sufficient for the existence of a positive equilibrium in the microfounded model. In contrast, $f > d$ is just a necessary condition in the conventional model. If $am < b$, such an equilibrium exists only if f is suitably bounded from above (cf. Kuang and Beretta, 1998, p. 392). Under such circumstances, equations (1) and (2) can generate entirely different dynamics. E.g., it is possible that the positive equilibrium E_2 is locally but not globally asymptotically stable, and one or both species could become extinct. Moreover, even limit cycles or heteroclinic cycles are possible (cf. Hsu et al., 2001). All these cases are excluded in the microfounded model.

If $f \leqq d$ (or $fc \leqq \gamma_2^{1/\alpha_2}$, respectively), the positive equilibrium disappears in both models. However, this case is rather irrelevant considering the microfounded model. Notice that $fc = \alpha_1 \bar{z}_1 e_2/(\beta_1 e_1)$ and that e_1, e_2 and α_1, β_1 should reasonably be of comparable magnitude, respectively, while $\bar{z}_1$, the maximum amount of biomass that the prey could use for transactions, should reasonably exceed the natural death rate of the predator, $\gamma_2 < 1$, raised to the power of $1/\alpha_2 \geqq 1$. Thus, the analysis of this case is merely of theoretical interest.

The microfounded model thus leaves no room for the empirically relevant case of species extinction, which is possible in case of the conventional model for $am < b$ even if $f > d$. This result shows that the economics approach to ecology, where species engage in a kind of maximization process, can resemble the dynamics of

settled biological models but adds more stability by excluding extinction. This phenomenon can be reintroduced, however, by taking Allee's Law into account. As the analysis of equations (6) and (7) has shown, adding the $A^i(n_i)$-functions leaves the dynamics unaltered for a region around the equilibrium with positive populations of both species but adds the possibility of extinction if the respective initial values are sufficiently small.

Appendix

A Continuity of (8) and (9) at the Origin

Using the definition of m, it is obvious that $n_1 e_1 + n_2 e_2 \leqq e_1(n_1 + m n_2)$ on R^2_+, from which

$$0 \leqq \frac{n_1 e_1 + n_2 e_2}{n_1 + m n_2} \leqq e_1.$$

Applying some transformations yields

$$-\gamma_1 n_1 \leqq n_1 \left[\left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1} - \gamma_1 \right] \leqq n_1 \left(\frac{r_0}{n_1} \right)^{\alpha_1} (c e_1)^{\beta_1} - \gamma_1 n_1.$$

As $n_1 \to 0$, both interval boundaries converge to zero if $0 < \alpha_1 < 1$. Thus,

$$\lim_{(n_1,n_2)\to(0,0)} n_1 \left[\left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1} - \gamma_1 \right] = 0,$$

proving continuity of (8) on R^2_+ if $\dot{n}_1 = 0$ for $n_1 = n_2 = 0$ by definition. Continuity of equation (9) is proven similarly.

B Derivation of (12)

The partial derivative of (8) with respect to n_1 evaluated at $\dot{n}_1 = 0$ is

$$\left. \frac{\partial \dot{n}_1}{\partial n_1} \right|_{\dot{n}_1 = 0} = \left(\beta_1 \frac{n_1 n_2 (m e_1 - e_2)}{(n_1 + m n_2)(n_1 e_1 + n_2 e_2)} - \alpha_1 \right) \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1} \tag{A1}$$

Using the definition of m, it follows that $m e_1 - e_2 = (\alpha_1 + \beta_1) e_2 / \beta_1 - e_2 = \alpha_1 e_2 / \beta_1 > 0$. Substituting into (A1) shows that the first term in parentheses and therefore the entire expression is negative.

The partial derivative of (8) with respect to n_2,

$$\frac{\partial \dot{n}_1}{\partial n_2} = \beta_1 \frac{n_1^2 (e_2 - m e_1)}{(n_1 + m n_2)(n_1 e_1 + n_2 e_2)} \left(\frac{r_0}{n_1} \right)^{\alpha_1} \left(\frac{c[n_1 e_1 + n_2 e_2]}{n_1 + m n_2} \right)^{\beta_1},$$

is negative since $e_2 - m e_1 < 0$.

Finally, it is straightforward that the partial derivatives of (9) are

$$\frac{\partial \dot{n}_2}{\partial n_1} = \frac{\alpha_2 m n_2^2}{n_1 (n_1 + m n_2)} \left(\frac{f c n_1}{n_1 + m n_2} \right)^{\alpha_2} > 0$$

and

$$\left. \frac{\partial \dot{n}_2}{\partial n_2} \right|_{\dot{n}_2 = 0} = -\frac{\alpha_2 m n_2}{n_1 + m n_2} \left(\frac{f c n_1}{n_1 + m n_2} \right)^{\alpha_2} < 0, \tag{A2}$$

proving (12). Notice that the signs of the cross partials are determined even off the isoclines.

C The Slope of (13)

Differentiation of

$$n_2 = \frac{\beta_1 e_1 n_1 \left[\bar{z}_1 - \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right]}{e_2(\alpha_1+\beta_1)\gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1} - \beta_1 \bar{z}_1 e_2}$$

with respect to n_1, letting D be an abbreviation for the denominator, yields:

$$\left.\frac{\partial n_2}{\partial n_1}\right|_{\dot{n}_1=0} = \frac{\left(\beta_1 e_1 \left[\bar{z}_1 - \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right] - \alpha_1 e_1 \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right) D}{D^2} - \frac{e_1 e_2 \alpha_1(\alpha_1+\beta_1)\gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\left[\bar{z}_1 - \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right]}{D^2}.$$

Recall relations (14) and (15). As the denominator is positive if $n_1 > \underline{n}_1$, this expression is negative if

$$\left(\beta_1 \left[\bar{z}_1 - \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right] - \alpha_1 \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right) D < e_2 \alpha_1(\alpha_1+\beta_1)\gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\left[\bar{z}_1 - \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}\right].$$

The right-hand side of this inequality is positive as $\bar{z}_1 > \gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1}$ if $n_1 < \overline{n}_1$. The left-hand side is negative as $n_1 > \underline{n}_1$ implies that $D > 0$ and $\beta_1 \bar{z}_1 - (\alpha_1+\beta_1)\gamma_1^{1/\beta_1}(n_1/r_0)^{\alpha_1/\beta_1} < 0$, respectively. This proves that the isocline $\dot{n}_1 = 0$ is negatively sloped if $\underline{n}_1 < n_1 < \overline{n}_1$.

D Exclusion of Closed Orbits

Applying Dulac's criterion (cf. Perko, 1996, p. 262) to equations (8) and (9), there is no closed orbit lying entirely in $R^2_{++} = \{(n_1, n_2) \in R^2 : n_1 > 0, n_2 > 0\}$ if there exists a function $B \in C^1(R^2_{++})$ such that the trace of the Jacobian of $(B\dot{n}_1, B\dot{n}_2)$ is not identically zero and does not change sign in R^2_{++}. Now consider the function $B = 1/(n_1 n_2)$. The partial derivative (A1) has been calculated under the assumption that $\dot{n}_1 = 0$, which has had just the effect that the term in square brackets in (8) has been omitted in (A1). Thus, it is straightforward that

$$\frac{\partial(B\dot{n}_1)}{\partial n_1} = \frac{1}{n_1 n_2}\left.\frac{\partial \dot{n}_1}{\partial n_1}\right|_{\dot{n}_1=0}$$

for all $(n_1, n_2) \in R^2_{++}$. An analogous argument shows that, using (A2),

$$\frac{\partial(B\dot{n}_2)}{\partial n_2} = \frac{1}{n_1 n_2}\left.\frac{\partial \dot{n}_2}{\partial n_2}\right|_{\dot{n}_2=0}$$

for all $(n_1, n_2) \in R^2_{++}$. As it follows from Appendix B that both expressions are negative, the trace of the Jacobian of $(B\dot{n}_1, B\dot{n}_2)$ is negative for all $(n_1, n_2) \in R^2_{++}$, proving that there are no closed orbits lying entirely in R^2_{++}.

E The Slope of (16)

Consider the region where $n_2^a < n_2 < \tilde{n}_2$. As the denominator of the derivative of (16) with respect to n_2 is positive, it suffices to consider the numerator, which is

$$(\gamma_2 \tilde{n}_2)^{1/\alpha_2} m \left[f c n_2^{1/\alpha_2} - (\gamma_2 \tilde{n}_2)^{1/\alpha_2}\right] - \frac{1}{\alpha_2} f c n_2^{1/\alpha_2} m (\gamma_2 \tilde{n}_2)^{1/\alpha_2}.$$

A sufficient condition for this expression to be negative is that $\alpha_2 \leqq 1$:

$$\begin{aligned} \alpha_2(\gamma_2\tilde{n}_2)^{1/\alpha_2} m\left[f c n_2^{1/\alpha_2} - (\gamma_2\tilde{n}_2)^{1/\alpha_2}\right] - f c n_2^{1/\alpha_2} m(\gamma_2\tilde{n}_2)^{1/\alpha_2} < 0 \\ \iff \qquad (\alpha_2 - 1) f c n_2^{1/\alpha_2} - \alpha_2(\gamma_2\tilde{n}_2)^{1/\alpha_2} < 0. \end{aligned}$$

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