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Interspecific Competition, Predation and Species Diversity: A Comment

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Motivated by a conjecture due to Paine (1966), Parrish & Saila (1970) recently investigated a simple mathematical model for a two prey–one predator system, seeking to show that the three-species system can be stable in circumstances where the two-prey system would in the absence of predation be unstable with respect to competition. Parrish & Saila in fact did not find such a three-species system, although they did show that the doomed prey species may persist longer with predation. We show that such three-species stable systems *can* be constructed under the model, and give examples illustrating the working of Paine's conjecture.

1. Introduction

It has been suggested (Hutchinson, 1961; Paine, 1966) that in some communities it may be that, although one particular trophic level would in isolation be unstable due to competition, the effects of other levels (e.g. predation) can lead to a total system which is stable.

Motivated by this idea, Parrish & Saila (1970) have recently made a numerical study of a simple mathematical model of a two prey–one predator system.† Beginning with two prey systems which are competitively unstable in the absence of predation, these authors carried out computations to see whether the inclusion of predation can render the three-species system stable, in the sense that all populations return to their equilibrium values if disturbed therefrom. However, the numerical coefficients they happened to choose always leave the total system in this sense unstable, even though the doomed prey species may move towards extinction more slowly than in the absence of predation. Thus Parrish & Saila's computer experiments do not strictly yield an example which illustrates Pain's conjecture.

In this paper we observe that it is possible to choose the numerical coefficients in Parrish & Saila's equations so that the three-species system is

† For a more detailed background account, see Parrish & Saila (1970, section 1, Introduction).

indeed stable, although the two-species system is not; and we give numerical examples which explicitly exhibit such behaviour.

The discussion in this paper is a particular application of a theoretical discussion of multi-species systems developed in a much wider context elsewhere (May, 1971), where it is shown that usually stability at any one trophic level goes with stability of the total trophic web, but that exceptions going either way (i.e. instability at one level with total web stability, as here; or alternatively stability at one level with total web instability) may be constructed with appropriate choice of parameters.

2. The Model

The equations of Parrish & Saila's (1970) model are

$$\frac{dN_1}{dt} = N_1[\varepsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3], \quad (1)$$

$$\frac{dN_2}{dt} = N_2[\varepsilon_2 - \alpha_{21}N_1 - \alpha_{22}N_2 - \alpha_{23}N_3], \quad (2)$$

$$\frac{dN_3}{dt} = N_3[-\varepsilon_3 + \alpha_{31}N_1 + \alpha_{32}N_2]. \quad (3)$$

Here N_1 and N_2 are the populations of the prey species, N_3 the predator population, and the various coefficients are as discussed in Parrish & Saila.

In the absence of predation ($N_3 = 0$) it is well known that the two-species system is unstable with regard to competition if

$$\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \leqslant 0 \quad (4)$$

and stable otherwise (e.g. Bartlett, 1960).

Starting with two-species systems which are unstable, Parrish & Saila make various choices of parameters for the three-species system, all of which happen to lead to total systems in which one of the prey species can be seen to be headed for extinction. However, an analytic investigation can be made of the general stability of the three-species system when it is displaced from equilibrium (e.g. May, 1971). The consequent stability behaviour is characterized by the roots of a cubic equation. In particular, it can be shown that under the condition of "equal predation" ($\alpha_{13} = \alpha_{23}$, $\alpha_{31} = \alpha_{32}$), which is considered throughout Parrish & Saila's paper, the total system is unstable if

$$\alpha_{11} + \alpha_{22} - \alpha_{12} - \alpha_{21} \leqslant 0. \quad (5)$$

All of Parrish & Saila's numerical choices satisfy both (4) and (5), with the consequences remarked above. But it is obviously possible to satisfy (4), as required, without satisfying (5). It is easier, moreover, to keep the total

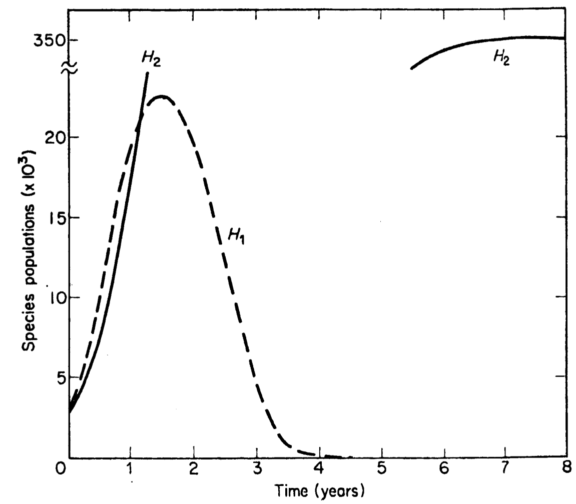

FIG. 1. Behaviour of the prey species populations, H_1 (------) and H_2 (———), in a competitive two-species system governed by equations (1) and (2) with coefficients having the proportions $\varepsilon_1 = 3$, $\varepsilon_2 = 2{\cdot}1$, $\alpha_{11} = 9\times10^{-5}$, $\alpha_{12} = \alpha_{21} = 3\times10^{-5}$, $\alpha_{22} = 0{\cdot}6\times10^{-5}$, $\alpha_{13} = \alpha_{23} = 0$. The initial conditions are $H_1(0) = H_2(0) = 3\times10^3$. The equilibrium value of H_2 is $3{\cdot}5\times10^5$.

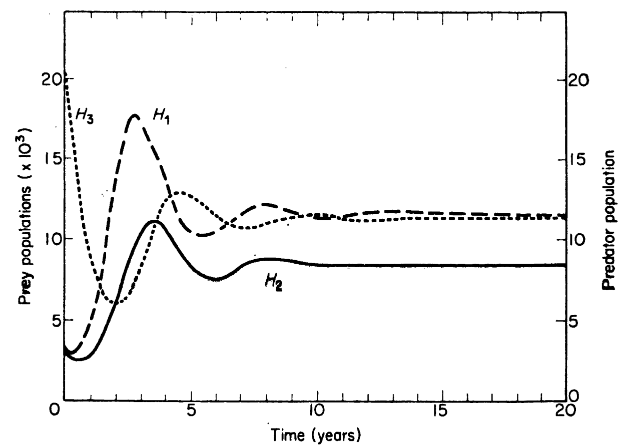

FIG. 2. Behaviour of the prey species populations, H_1 (------) and H_2 (———), and the predator population, H_3 (......) in the three-species system corresponding to the two-species system of Fig. 1. Equations (1) and (2) have coefficients with the same proportions as in Fig. 1, except for $\alpha_{13} = 0{\cdot}15$, $\alpha_{23} = 0{\cdot}15$, and the coefficients of equation (3) have proportions $\varepsilon_3 = 1{\cdot}2$, $\alpha_{31} = \alpha_{32} = 0{\cdot}6\times10^{-4}$. The initial conditions of H_1, H_2, H_3 respectively are 3×10^3, 3×10^3 and 20, and the equilibrium values are respectively 11·66, 8·34 and 1·13.

system stable even though (4) is fulfilled if the artificial condition of "equal predation" is not required.

In Fig. 1 we show a competitively unstable two-prey system in the absence of a predator: the parameters are given in the figure caption. Restricting ourselves to "equal predation", we see in Fig. 2 that the corresponding three-species system can be stable, with all populations returning to their equilibrium values if displaced: the interaction parameters are again catalogued in the caption. Notice that the interaction parameters used in Figs 1 and 2 are within the ranges of those used in Parrish & Saila's paper.

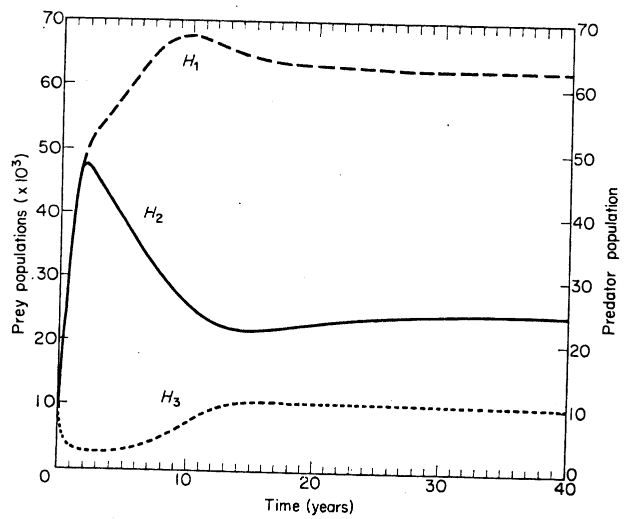

FIG. 3. Behaviour of the prey species populations, H_1 (------) and H_2 (——), and the predator species population H_3 (......) in the three-species system with unequal predation (corresponding to the two-species system of Fig. 6 of Parrish & Saila). Equations (1) to (3) have coefficients with the proportions $\varepsilon_1 = \varepsilon_2 = 3{\cdot}22$, $\alpha_{11} = 0{\cdot}9 \times 3{\cdot}22 \times 10^{-5}$, $\alpha_{12} = \alpha_{21} = \alpha_{22} = 3{\cdot}22 \times 10^{-5}$, $\alpha_{13} = 0{\cdot}06$, $\alpha_{23} = 0{\cdot}04$, $\varepsilon_3 = 2{\cdot}25$, $\alpha_{31} = 3 \times 10^{-5}$, $\alpha_{32} = 10^{-5}$. The initial conditions of H_1, H_2, H_3 respectively are 10^4, 10^4 and 10, and the equilibrium values are respectively 62·5, 24·9 and 1·01.

The three-species system depicted in Fig. 3 is a case where the two-prey system in the absence of predation is exactly as in Fig. 6 of Parrish & Saila (i.e. $\alpha_{11} = 0{\cdot}9\alpha_{22}$; $\alpha_{22} = \alpha_{12} = \alpha_{21}$), where N_2 is essentially extinct after 20 years. Now, allowing unequal predation, we can arrive at a corresponding three-species system which is fully stable, as shown in Fig. 3: this is a possible alternative to the (unstable) three-species system given in Parrish & Saila's Fig. 7.

3. Discussion

Using the simple three-species mathematical model of Parrish & Saila (1970), we go beyond their work to illustrate some examples where indeed the three-species system is fully stable, all populations returning to their equilibrium values if disturbed, even though the two-species prey system is in isolation unstable due to competition.

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