ROCKY MOUNTAIN
JOURNAL OF MATHEMATICS
Volume 12, Number 4, Fall 1982

PREDATOR INFLUENCE ON THE GROWTH OF A POPULATION WITH THREE GENOTYPES II

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Dedicated to Professor Lloyd K. Jackson
on the occasion of his sixtieth birthday.

1. Introduction. The system of ordinary differential equations

$$
(1.1)\qquad
\begin{aligned}
x_1' &= (x_1 + (1/2)x_2)^2/x^2)\, B(x) - (\varDelta(x) + yP_1(x, y))(x_1/x) \\
x_2' &= (2(x_1 + (1/2)x_2)(x_3 + (1/2)x_2)/x^2)B(x) \\
&\qquad - (\varDelta(x) + yP_2(x, y)\,(x_2/x) \\
x_3' &= ((x_3 + (1/2)x_2)^2/x^2)\, B(x) - (\varDelta(x) + yP_3(x, y))(x_3/x) \\
y' &= y(-s + k \sum_{i=1}^{3} P_i(x, y)) \\
x_i(0) &= x_{i0} > 0, y(0) = y_0 > 0, x = x_1 + x_2 + x_3
\end{aligned}
$$

was investigated in [11] as a model of a predator, denoted by y, feeding on a prey, denoted by x, which consists of three genotypes, denoted by x_1, x_2, x_3, corresponding to a one locus, two allele, genetic model. Without the predator, this system of equations also appears in [1] and [5]. In the genetics literature these three genotypes are frequently denoted by *AA*, *Aa*, *aa*, emphasizing the two choices for each allele at the distinguished location. If one of the genetic characteristics is recessive, the organism will appear as two varieties, called phenotypes, and the resulting difference, say color [3], may affect the susceptibility of the organism to predation.

Standard hypotheses to model the predator-prey relationship (intermediate type models in the language of [9]) are:

$$
\text{(H-1)}\qquad
\begin{aligned}
&\varDelta(x) \geqq 0,\ B(0) = \varDelta(0) = 0,\ B'(0) > \varDelta'(0) \geqq 0. \\
&\text{If } y > 0,\ P_i(x, y) = 0 \Leftrightarrow x = 0,\ P_{ix}(x, y) > 0.
\end{aligned}
$$

[1]Research supported by Natural Science and Engineering Research Council of Canada Grant NSERC A-4823.

[2]Research supported by NSF grant MCS-7901069. A portion of this work was completed while this author was a Visiting Professor at the University of Utah, Salt Lake City, Utah

Received by the editors on May 29, 1981.

(H-2) There exists a unique positive number K, (the carrying capacity) such that $B(K) = \Delta(K) > 0$ and $B'(K) < \Delta'(K)$. If $y(t)$ were not present, i.e., $y(t) = 0$, the system (1.1) would reduce to

$$x' = B(x) - \Delta(x)$$

a standard growth model. In [11] the following two additional assumptions were made:

(H-4) $P_1(x, y) = P_2(x, y) \geqq 0$,

$$\inf_{\substack{K \geqq x > 0 \\ M \geqq y > 0}} \frac{P_1(x, y) - P_3(x, y)}{x} \geqq \delta(M) > 0.$$

(H-5) The system

$$x' = B(x) - \Delta(x) - yP_3(x, y),$$
$$y' = y(-s + kP_3(x, y)),$$

has a globally (with respect to the open positive quadrant) asymptotically stable critical point (x^*, y^*), $x^* > 0$, $y^* > 0$.

(H-5) expresses the fact that the predator can survive on the most difficult to capture (in view of H-4) prey. Such a hypothesis holds, for example, in **[8]** **[10]** **[13]**. With these assumptions it was shown that $\lim_{t \to \infty} x_i(t) = 0$, $i = 1, 2$, $\lim_{t \to \infty} x_3(t) = x_3^* > 0$ and $\lim_{t \to \infty} y(t) = y^* > 0$.

In this paper we replace (H-4) and (H-5) by

(H-4)′ $P_1(x, y) = P_2(x, y)$,

$$\inf_{\substack{K \geqq x > 0 \\ M \geqq y > y^*}} \frac{P_3(x, y) - P_1(x, y)}{x} \geqq \delta(M) > 0.$$

where y^* is defined in (H-5)′, below.

(H-5)′ The system

(1.2)
$$x' = B(x) - \Delta(x) - yP_1(x, y),$$
$$y' = y(- +s\, kP_1(x, y)),$$

has a globally (with respect to the open positive quadrant) asymptotically stable critical point (x^*, y^*), $x^* > 0$, $y^* > 0$.

The reversed inequality in (H-4)′ makes x_1 the more difficult to capture prey while retaining the hypothesis that x_1 and x_2 are the same phenotype (H-5)′ has the same biological interpretation as before—the roles of

x_1 and x_3 are merely reversed. Note that in (H-4)′ the infimum is being taken over a smaller set than in (H-4). This allows for a wider class of predation functions. In particular it allows for a polynomial in y which is precluded in (H-4).

With the reversal of the inequality in (H-4) one anticipates that the phenotype given by the dominant gene will survive, although the proof given in [11] breaks down. We, in fact, show more—that the inequality (H-4)′ leads to the survival of only the homozygote, x_1. Thus predation inequalities like (H-4) or (H-4)′ lead to the evolution of a "pure strain". Stated in another way, one has that if a polymorphism evolves, it is not due to only the influence of greater susceptibility to predation in that habitat.

Other papers involving both a genetic and an ecological component may be found in [4], [6], [12].

2. Results. Our principal result may now be stated.

THEOREM 1. *Suppose* (H-1), (H-2), (H-4)′, H(5)′ *hold. Then*

$$\lim_{t\to\infty} x_1(t) = x^* > 0,$$

$$\lim_{t\to\infty} x_i(t) = 0, \quad i = 2, 3,$$

$$\lim_{t\to\infty} y(t) = y^* > 0,$$

where (x^*, y^*) *is the critical point given in* (H-5)′.

Before beginning the proof we note that in [11] it was assumed a priori that the predator survived, i.e., $\limsup_{t\to\infty} y(t) > 0$. We show that (H-4)′ is sufficient for this purpose, so that this assumption need not be made. Denote the right hand side of (1.2) by $f(x, y)$, $g(x. y)$, i.e.,

$$x' = f(x,y),$$
$$y' = g(x,y).$$

Using (H-4)′, adding equations in (1.1), and denoting x and y there by $\bar{x}$, $\bar{y}$, one has

$$\bar{x}' \leqq f(x,y),$$
$$\bar{y}' \geqq g(x,y).$$

Let $z = -y$, $\bar{z} = -\bar{y}$. The two systems become

$$x' = f(x,-z),$$
$$z' = -g(x,-z).$$

and

$$\bar{x}' \leqq f(x, -\bar{z}),$$
$$\bar{z}' \leqq -g(x, -\bar{z}).$$

Now $\partial f/\partial y = -P_1(x, y) < 0$ and $\partial(-g)/\partial x = kx(\partial P_1/\partial x) < 0$ for $z < 0$, or the right hand sides satisfy condition K [7, p. 27] and hence, if the initial conditions are the same, $\bar{x}(t) \leqq x(t)$, $\bar{z}(t) \leqq z(t)$ for all $t > 0$. Therefore $\bar{y}(t) \geqq y(t)$ and since $\lim_{t\to\infty} y(t) = y^* > 0$, it cannot be the case that $\limsup_{t\to\infty} y(t) = 0$.

This particular device can be used in general to yield a component-wise corollary of Kamke's Theorem for general systems, as general for example, as given in [7, p. 29].

For reference, we state our result as follows.

LEMMA 1. $\liminf_{t\to\infty} y(t) \geqq y^*$.

A portion of the proof of the theorem follows that given in **[11]**. We begin with four lemmas, the first three of which follow as in **[11]** since they involve only (H-1)–(H-2).

LEMMA 2. *All solutions of* (1.1) *with initial conditions in the region* $T = \{(x_1, x_2, x_3, y) \mid x_i \geqq 0, i = 1, 2, 3, y \geqq 0, x_1 + x_2 + x_3 \leqq K\}$ *are bounded and hence can be continued to a half line.*

LEMMA 3. *There are no interior* (*to the positive cone*) *critical points for* (1.1).

LEMMA 4. *No trajectory of* (1.1) *has an omega limit point of the form* $(\tilde{x}_1, \tilde{x}_2, 0, y)$ *with* $\tilde{x}_2 > 0$.

LEMMA 5. *Let* $(x_1(t), x_2(t), x_3(t), y(t))$ *be a solution of* (1.1). *If* $x_3 y \notin L_1(R^+)$, *this solution has the asymptotic behavior described in the theorem.*

PROOF. Suppose $(x_3 y)(t) \notin L_1(\mathbf{R}^+)$ and let

$$u(t) = x_1(t) + \frac{1}{2}x_2(t),$$

$$v(t) = x_3(t) + \frac{1}{2}2x_2(t).$$

Then

$$v'/v - u'/u = (yx_3/xv)(P_1(x, y) - P_3(x, y))$$

and hence, using (H-4)′

$$0 \leqq v(t) \leqq cu(t)\exp((-\delta/K)\int_{t_0}^{t} x_3(s)y(s)ds)$$

for t_0 sufficiently large. If $x_3 y \notin L_1(\mathbf{R}^+)$, then $\lim_{t\to\infty} v(t) = 0$. The remainder of the proof follows that of Lemma 3.3 of **[11]**.

PROOF OF THEOREM 1. Let $\Gamma(t) = (x_1(t), x_2(t), x_3(y), y(t))$. In view of Lemma 5 one may suppose that $(x_3 y)(t) \in L_1(\mathbf{R}^+)$. Since $(x_3 y)'(t)$ is bounded, $\lim_{t\to\infty}(x_3 y)(t) = 0$.

If $\lim\sup_{t\to\infty} x_3(t) = \alpha > 0$, then there is a subsequence t_n such that $\lim_{n\to\infty} x_3(t_n) = \alpha > 0$. Therefore $\lim_{n\to\infty} y(t_n) = 0$ or $\lim\inf_{t\to\infty} y(t) = 0$. This is impossible by Lemma 1. If $\lim\sup_{t\to\infty} x_3(t) = 0$, then, in view of Lemma 4, $\lim_{t\to\infty} x_2(t) = 0$. The omega limit set is two dimensional—it lies in the x_1, y plane—and hence must consist of trajectories of (1.2). However, by (H-5)$'$ all trajectories in the positive quadrant tend to the critical point (x^*, y^*). This completes the proof.

We note that similar improvement can be made on Theorem 3.1 of **[11]**. We state this as follows.

THEOREM 2. *Suppose* (H-1)–(H-2), (H-5) *holds and that*

(H4)$''$ $$\inf_{\substack{M\geq y\geq y^* \\ K\geq x>0}} \frac{P_1(x, y) - P_3(x, y)}{x} \geqq \delta(M) > 0.$$

Then

$$\lim_{t\to\infty} x_i(t) = 0, \quad i = 1, 2,$$
$$\lim_{t\to\infty} x_3(t) = x^* > 0,$$
$$\lim_{t\to\infty} t(y) = x^* > 0.$$

PROOF. In view of Lemma 1 the hypothesis that the predator survives is not necessary. The change in the proof of Lemma 5 above can be made in Lemma 3.3 of **[11]**. The proof can then follow as in **[11]**.

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