数理解析研究所講究録
第 457 巻 1982 年 44-53

Predator - Prey ボルテラモデルにおける進化の特徴

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1. Introduction

Allen (1975) studied the evolution of a predator- prey Volterra-Lotka model without saturation effect for the case where either predator or prey evolves, and also studied a simpler case with saturation effect of prey (1976). This paper is an extension of his first paper (1975), i.e., this paper studies the evolution of a predator-prey Volterra-Lotka model with saturation effect for the general case where both predator and prey evolve.

We investigate the following points.

1) A sufficient condition of evolution.
2) Properties of population change under the evolutional condition.
   Predator population and the ratio of predator to prey populations always increase. Increase of the ratio of predator to prey populations was predicted in the paper by Allen (1975) for an ecosystem without saturation.
3) Macroscopic trace of parameters under the evolutional condition.
   The parameters of the prey drift in the direction of increasing multiplication rate and saturation level. The parameters of the drift in the direction of decreasing death rate.

2. Model of Evolution

The equations before the appearance of a mutation are assumed to be

$$\frac{dX}{dt} = X \, (A - BY - CX) \tag{1}$$

$$\frac{dY}{dt} = Y \, (-D + EX - FY) \tag{2}$$

where A,B,C,D,E and F are positive, and AE>CD, i.e., the equilibrium of Y is positive. X is the prey population and Y is that of the predator.

We assume that mutations of the prey and the predator appear at time t_0 simultaneously. The equations governing the mutant populations are

$$\frac{dx}{dt} = x \, [\, a - b \, (Y + y) - c \, (X + x) \,] \tag{3}$$

$$\frac{dy}{dt} = y \, [\, -d + e \, (X + x) - f \, (Y + y) \,] \tag{4}$$

where a,b,c,d,e and f are positive. x is the mutation of the prey and y is one of the predator. We assume simultaneity of appearance of mutations of the prey and the predator for simplicity, however it is not essential under discussion below and the same results hold. After the appearance of mutation, X and Y change according to

$$\frac{dX}{dt} = X \, [\, A - B \, (Y + y) - C \, (X + x) \,] \tag{5}$$

$$\frac{dY}{dt} = Y \, [\, -D + E \, (X + x) - F \, (Y + y) \,] \tag{6}$$

This step is repeated many times in real evolution.

3. Condition of Evolution

From (3) and (5) we can deduce that

$$\frac{b}{X}\frac{dX}{dt} - \frac{B}{x}\frac{dx}{dt} = (Ab - aB) - (bC - Bc)(X + x) \tag{7}$$

and on integration this gives

$$\frac{[\ X(t)\ ]^{b}}{[\ x(t)\ ]^{B}} = \frac{[\ X(t_0)\ ]^{b}}{[\ x(t_0)\ ]^{B}} \exp \Big[- AB \Big(\frac{a}{A} - \frac{b}{B} \Big) t$$

$$- BC \Big(\frac{b}{B} - \frac{c}{C} \Big) \int_{t_0}^{t} [\ X(\tau) + x(\tau)\ ] d\tau \Big] \tag{8}$$

Now, we can see that x, y, X and Y are finite and all of them do not go to zero from (3) and (4). Therefore from (8) it follows that though $x(t_0)$ is only an infinitesimal fluctuation from zero, the system amplifies it until x has completely replaced X provided that $a/A > b/B > c/C$ holds, because $x(t)$ is bounded from above.

From (4) and (6) we can get the following equation in the same way as (8):

$$\frac{[\ Y(t)\ ]^{f}}{[\ y(t)\ ]^{F}} = \frac{[\ Y(t_0)\ ]^{f}}{[\ y(t_0)\ ]^{F}} \exp \Big[- DF \Big(\frac{f}{F} - \frac{d}{D} \Big) t$$

$$- EF \Big(\frac{e}{E} - \frac{f}{F} \Big) \int_{t_o}^{t} [\ X(\tau) + x(\tau)\ ]\ d\tau \Big] \tag{9}$$

Equation (8),(9), and the boundedness of X,Y,x and y yield the following proposition which gives a sufficient condition of evolution.

<u>Proposition 1</u>

If $$\frac{a}{A} > \frac{b}{B} > \frac{c}{C} \tag{10}$$

and $$\frac{e}{E} > \frac{f}{F} > \frac{d}{D} \tag{11}$$

are satisfied, then the prey and the predator evolve, i.e., x replaces X and y replaces Y.

Proposition 1 shows a sufficient condition for the general case where both predator and prey evolve. When we study the evolution of either prey or predator alone, (10) is a sufficient condition of the evolution of the prey and (11) is that of the evolution of the predator. The condition in Proposition 1 we shall refer to as *evolutional condition*.

Corollary 1

If $\frac{a}{A} < \frac{b}{B} < \frac{c}{C}$ (12)

and $\frac{e}{E} < \frac{f}{F} < \frac{d}{D}$ (13)

are satisfied, then the evolution of the predator and the prey cannot occur, i.e. x and y are rejected.

This can be easily derived in the same way as Proposition 1.

Corollary 1 shows a condition for predator and prey not to evolve.

4. Properties of the Population Movement under Evolution

An equilibrium of ecosystem before evolution equations (1) and (2) is

$$P_b = (X^{\circ} \; Y^{\circ}) = \left(\frac{AF + BD}{CF + BE} \quad \frac{AE - CD}{CF + BE} \right) \tag{14}$$

If the equilibrium is positive, X and Y generally tend to P_b asymptotically from any positive initial state. Unfortunately, we cannot prove that the system has no limit cycle. If it does exist, it is around P_b. Therefore it is reasonable that we value the population movement under evolution through the value of the equilibrium. We compare an equilibrium before the evolution with one after that in this section. This step of the evolution repeats many times in real ecosystem.

4.1. Evolution of The Prey Alone

After x replaced X, i.e. the prey evolved, the equations governing the system are

$$\frac{dx}{dt} = x \, (a - bY - cx) \tag{15-a}$$

$$\frac{dY}{dt} = Y\ (- D + Ex - FY\ ) \qquad (15\text{-}b)$$

An equilibrium is

$$P_a = (\ \bar{x}\ \bar{Y}\ ) = (\ \frac{aF + bD}{cF + bE}\ \frac{aE - cD}{cF + bE}\ ) \qquad (16)$$

Comparison between (14) and (16) under the evolutional condition yields the following proposition.

<u>Proposition 2</u>

(i) $Y^\circ < \bar{Y}$ (17)

(ii) $Y^\circ / X^\circ < \bar{Y} / \bar{x}$ (18)

(iii) $X^\circ < \bar{x}$ (19)

Part (i) in Proposition 2 shows that the predator population increases under the evolutional condition; (ii) shows that the ratio of predator to prey populations increases under the evolutional condition; and (iii) shows that the prey population increases under the evolutional condition.

4.2. Evolution of The Predator Alone

After y replaced Y, i.e. the predator evolved, the equations governing the system are

$$\frac{dX}{dt} = X\ (\ A - By - CX\ ) \qquad (20\text{-}a)$$

$$\frac{dy}{dt} = y\ (\ -d + eX - fy\ ) \qquad (20\text{-}b)$$

An equilibrium is

$$P_a = (\ \bar{X}\ \bar{y}\ ) = (\ \frac{Af + Bd}{Cf + Be}\ \frac{Ae - Cd}{Cf + Be}\ ) \qquad (21)$$

Comparison between (14) and (21) under the evolutional condition yields the following proposition.

Proposition 3

(i) $Y^{\circ} < \bar{y}$ (22)

(ii) $Y^{\circ}/ X^{\circ} < \bar{y} / \bar{X}$ (23)

(iii) $X^{\circ} > \bar{X}$ (24)

Part (i) in Proposition 3 shows that the predator population increases under the evolutional condition; (ii) shows that the ratio of predator to prey populations increases under the evolutional condition; and (iii) shows that the prey population decreases under the evolutional condition.

4.3. Evolution of Both Prey and Predator

After x replaced X and y replaced Y, i.e. both prey and predator evolved, the equations governing the system are

$$\frac{dx}{dt} = x\ (\ a - by - cx\ ) \qquad (25\text{-a})$$

$$\frac{dy}{dt} = y\ (\ - d + ex - fy\ ) \qquad (25\text{-b})$$

An equilibrium is

$$P_a = (\ \bar{x}\ \bar{y}\ ) = (\ \frac{af + bd}{cf + be}\ \frac{ae - cd}{cf + be}\ ) \qquad (26)$$

Comparison between (14) and (26) under the evolutional condition yields the following proposition.

Proposition 4

(i) $Y^{\circ} < \bar{y}$ (27)

(ii) $Y^{\circ}/ X^{\circ} < \bar{y} / \bar{x}$ (28)

Part (i) shows that the predator population increases under the evolutional condition; and (ii) shows that the ratio of predator to prey populations increases under the evolutional condition.

4.4. Common Properties

From Proposition 2-4, properties of the population movement under the evolutional condition are derived as follows.

Proposition 5

Predator populations and the ratio of predator to prey populations always increase under the evolutional condition.

The increase of the ratio of predator to prey populations was predicted in Allen's (1975) paper for an ecosystem without saturation. An example, perhaps, of this property is that the ratio of consumer to producer biomass in the ocean is surprisingly high considering the efficiency of photosynthetic plankton (Allen, 1975).

5. Macroscopic Trace of Parameters under Evolution

In Proposition 1 we studied a condition of one step of evolution. Now let us investigate the path traced by the parameters in parameter space through several steps of evolution.

The parameter space of the prey and that of the predator are considered separately. In Figures 1-a and 1-b each relation of two

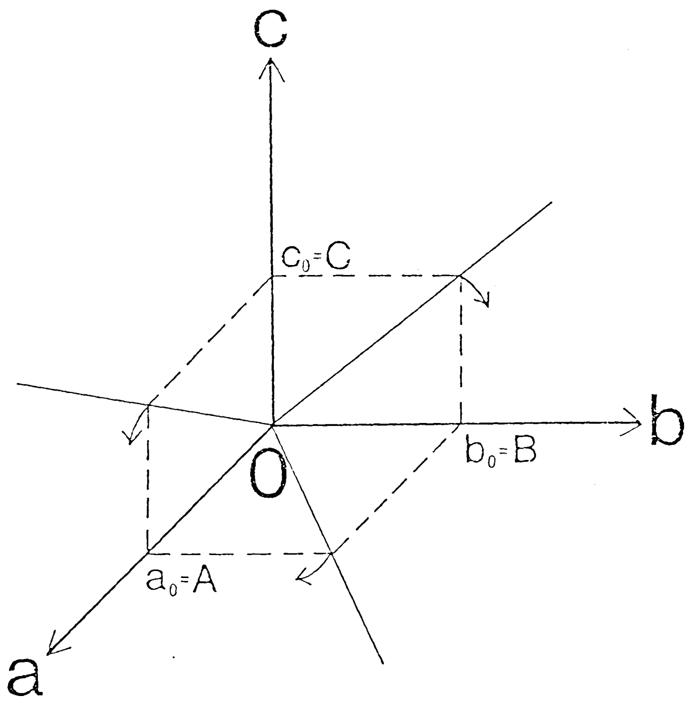

Figure1-a. Relation of two parameters (a-b, b-c, c-a).

parameters from (10) and (11) are shown. In Figure 1-a the direction of movement of b in the a-b plane is opposite to that in the b-c plane. We may consider, therefore, that the main variation of parameters occurs between a and c and that the variation of b is small. Similary, in Figure 1-b the main variation occurs between d and e and that of f is small. From the abovementioned, the trace of b and e signify the rate of capturing prey by predator. Therefore, b and e do not have large change. This agrees with the idea an *arms race*, where successive improvements in the avoidance

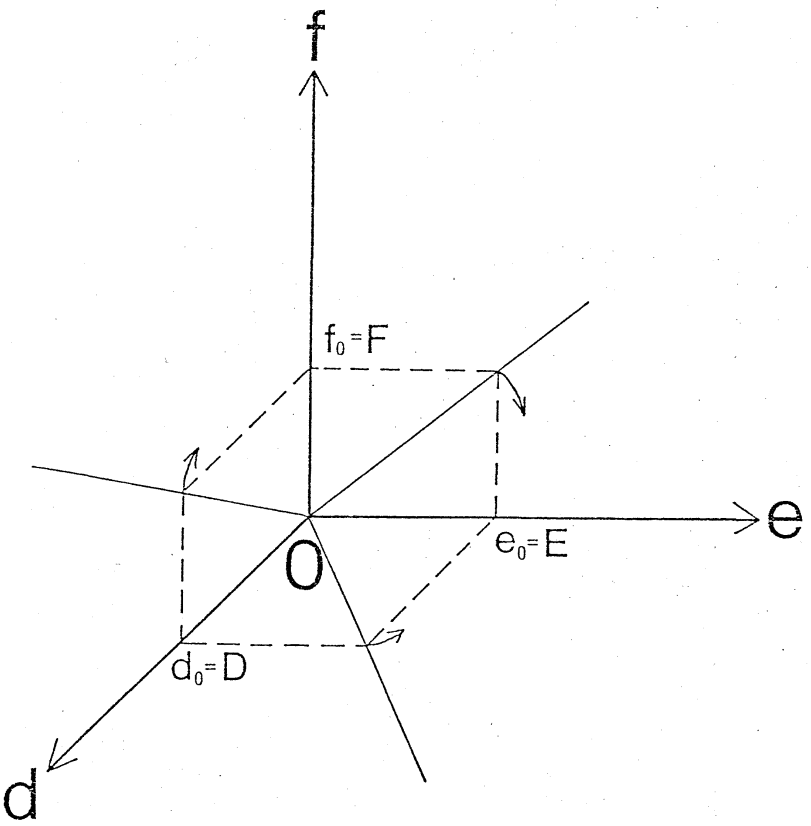

Figure 1-b. Relation of two parameters (d-e, e-f, f-d).

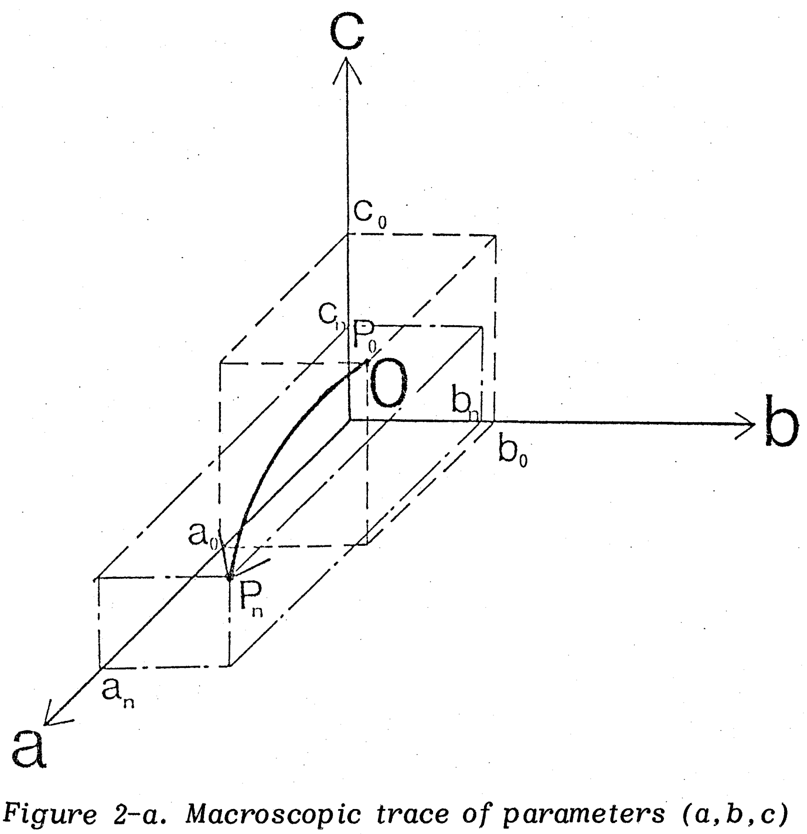

Figure 2-a. Macroscopic trace of parameters (a, b, c) under evolution.

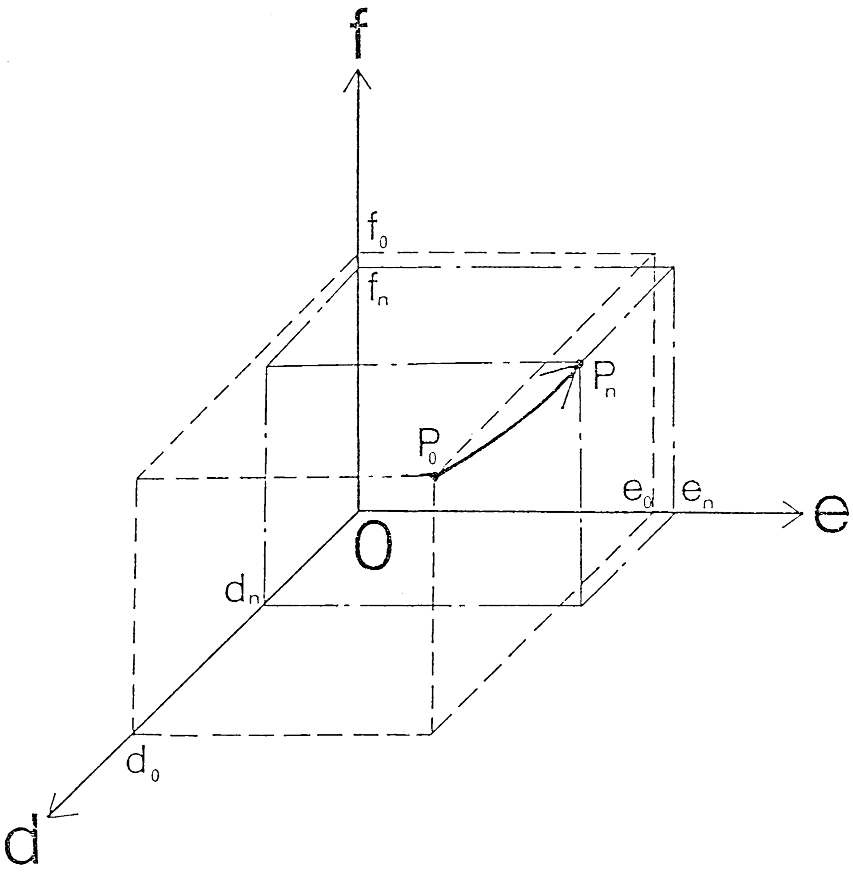

Figure 2-b. Macroscopic trace of parameters (d,e,f) under evolution.

technique of the prey, as suggested by Allen (1976).

Consequently, the macroscopic trace of parameters under evolution are shown as Figures 2-a and 2-b; $a_0, \cdots, f_0$ are initial values and $a_n, \cdots, f_n$ are values after n steps. In Figure 2-a the parameters of the prey drift in the direction of increasing multiplication rate and saturation level. In Figure2-b the direction of drift of the parameters of the predator is one of decreasing death rate.

6. Conclusion

We discussed the evolution of a predator-prey Volterra-Lotka model with saturation effect. The predator population and the ratio of predator to prey populations always increase under the evolutional condition, i.e. under the evolution of the prey alone, that of the predator alone, and that of both prey and predator. The parameters of the prey drift in the direction of increasing multiplication rate and saturation level. The direction of the drift of the parameters of the predator is one of decreasing death rate.

References

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This paper will be published in Bull. Math. Biol..