Persistence of Altruistic Community under Indiscriminate Altruism

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ABSTRACT

The evolution of indiscriminate altruism in animal populations is examined using coupled Von Foerster equations. Analytic expression for the gene frequency of altruists is derived. We also obtain formulas for the numbers of the altruistic and nonaltruistic groups at each generation in terms of the age-dependent ratio of altruists in the population during each generation, $f_n(a)$. We then use our results to demonstrate the distinction between the evolution of altruism and the survival of an altruistic society, and our discussion is then illustrated with simulated examples.

Keywords: indiscriminate altruism, altruistic frequency, semelparous population, Von Foerster equations, persistence

I. Introduction

The evolution of an altruistic trait in a biological population (e.g. alarm calls, fending off of all intruders) despite its obvious disadvantage to the altruistic individual is a subject of interest in population genetics. The earlier work included Hamilton (1964), Maynard Smith (1965), Trivers (1971), etc. More recently, the subject has been discussed by Cavalli-Sforza and Feldman (1978, 1981), Maynard Smith (1980) and Akin (1984). There are generally two theories: one is reciprocal altruism (Trivers, 1971) where the altruistic act is performed in favor of other altruists; the other is kin selection (Hamilton, 1964) where the relatives of an altruist are favored.

In Hsieh (1988), a model of coupled Von Foerster equations was proposed to examine the evolution of an altruistic community with age-dependent altruism. Assuming the population is semelparous with the length of a lifetime fixed at $a_f > 0$, the model is as follows:

$$D\alpha(a,t) + \rho_1(\alpha(a,t),\beta(a,t),a) = 0, \quad (1.1)$$

$$D\beta(a,t) + \rho_2(\alpha(a,t),\beta(a,t),a) = 0, \quad 0 \leqslant a \leqslant a_f \quad (1.2)$$

with

$$\alpha(0,t) + \beta(0,t) = \bar{F}(\alpha(a_f,t) + \beta(a_f,t)). \quad (1.3)$$

Here $\alpha(a,t)$, $\beta(a,t)$ are the numbers of altruistic and selfish members of the population of age a at time t, respectively, $\bar{F}$ is the fecundity function and

$$\rho_1(\alpha,\beta,a) = \pi_1^\alpha(a)\alpha + \pi_2(a)\alpha(\alpha+\beta)$$
$$- \gamma_\alpha(a)\frac{\alpha}{\alpha+\beta}\alpha, \quad (1.4)$$

$$\rho_2(\alpha,\beta,a) = \pi_1^\beta(a)\beta + \pi_2(a)\beta(\alpha+\beta)$$
$$- \gamma_\beta(a)\frac{\alpha}{\alpha+\beta}\beta \quad (1.5)$$

are the loss functions. Moreover, π_1^α and π_1^β are age-dependent mortality and migration rates, and π_2 denotes the crowding factor, while γ_α and γ_β are the net benefit each group receives due to altruism.

Note that no a priori assumption is made on the altruistic functions γ_α and γ_β, although a condition of $\gamma_\alpha(a) > \gamma_\beta(a)$ would imply reciprocal altruism in the population. The only condition imposed so far is that π_1^α and π_1^β are continuous and nonnegative in $[0,a_f]$.

Making use of results in Coffman and Coleman (1979), we can obtain sufficient conditions on the altruistic functions and fecundity function $\bar{F}$ to ensure the evolution of altruism (see Hsieh, 1988). However, analytic expressions for the altruistic ratio in the population or the size of the altruistic group can not be obtained.

In this paper, we shall attempt to find analytic formulas for the population at each generation by making the additional assumption of indiscriminate altruism (i.e. $\gamma_\alpha = \gamma_\beta$). This assumption is valid for altruistic acts shared equally by all members of the population (although this is obviously not an appropriate assumption when one describes the intricate systems of designated work in communities of social insect).

Sections 2 and 3 are devoted to finding an analytic solution of the system described in (1.1)-(1.5), assuming indiscriminate altruism. The biological significance of the results will be given in Section 4 along with simulated examples to illustrate the conclusions.

II. Evolution of Altruism under Indiscriminate Altruism

In this section we shall make the additional assumption that the benefit of altruistic behavior is shared and shared alike by all individuals of the population, hence $\gamma_\alpha(a) = \gamma_\beta(a) = \gamma(a)$. In this case, condition (4.2) in Hsieh (1988) is always satisfied, and thus, altruism will evolve under appropriate conditions on the fecundity function $\bar{F}$.

Following the procedure used in Hsieh (1988), we let $a_f = 1$ and $x_n(a) = \alpha(a, n+a)$, $y_n(a) = \beta(a, n+a)$. Suppressing the subscripts in x_n and y_n to simplify the typography in this section, we can rewrite (1.1), (1.2) as

$$x'(a) + \pi_1^\alpha(a)x(a) + \pi_2(a)x(a)[x(a)+y(a)]$$

$$- \gamma(a)\frac{x(a)}{x(a)+y(a)} x(a) = 0, \qquad (2.1)$$

$$y'(a) + \pi_1^\beta(a)y(a) + \pi_2(a)y(a)[x(a)+y(a)]$$

$$- \gamma(a)\frac{x(a)}{x(a)+y(a)} y(a) = 0, \quad \text{for } 0 \leqslant a \leqslant 1. \quad (2.2)$$

Adding the above equations, we get

$$z'(a) + \pi_1^\alpha(a)x(a) + \pi_1^\beta(a)[z(a)-x(a)]$$

$$+ \pi_2(a)z^2(a) - \gamma(a)x(a) = 0 \qquad (2.3)$$

where $z(a) = x(a) + y(a)$ is the total population size. Multiplying (2.1) and (2.3) by $z(a)$ and $x(a)$, respectively, and subtracting, we get

$$x'z - z'x - \hat{\pi}_1(a)(z-x)x = 0 \qquad (2.4)$$

where

$$\hat{\pi}_1(a) = \pi_1^\beta(a) - \pi_1^\alpha(a). \qquad (2.5)$$

Dividing (2.4) by $z^2(a)$ and let $f(a) = x(a)/z(a)$ be the proportion of altruists in the population, we get a separable equation:

$$f'(a) = \hat{\pi}_1(a)f(a)[1 - f(a)], \quad 0 \leqslant a \leqslant 1. \qquad (2.6)$$

The solution to (2.6) is simply

$$f(a)/[1 - f(a)] = \left\{ f(0)/[1 - f(0)] \right\} \exp[\int_0^a \hat{\pi}_1(\tau)d\tau] \qquad (2.7)$$

with $f(0)$ the initial ratio of altruists in the community.

Since $1 - f(a) = y(a)/z(a)$, (2.7) can be written as

$$x(a)/y(a) = \left\{ x(0)/y(0) \right\} \exp[\int_0^a \hat{\pi}_1(\tau) d\tau]. \qquad (2.8)$$

Going back to the notation in Section 1, we have

$$\frac{\alpha(a, n+a)}{\beta(a, n+a)} = \frac{\alpha(0,n)}{\beta(0,n)} \exp[\int_0^a \hat{\pi}_1(\tau) d\tau] \qquad (2.9)$$

the ratio between the altruists and nonaltruists of age a at the n-th generation.

Let $p_n = \alpha(1, n+1)/\beta(1, n+1)$ be the ratio of adult altruists and nonaltruists of n-th generation prior to reproduction, we have the following formula:

$$p_n = G(p_{n-1}) \exp[\int_0^1 \hat{\pi}_1(\tau) d\tau], \qquad (2.10)$$

where

$$G(p_{n-1}) = G(\frac{\alpha(1,n)}{\beta(1,n)}) = \frac{\alpha(0,n)}{\beta(0,n)} \qquad (2.11)$$

is the "fecundity function" for the ratio of successive generations of altruists and nonaltruists. Moreover, since

$$q_{n-1}^2(1) = \frac{\alpha(1,n)}{\alpha(1,n) + \beta(1,n)} = \frac{p_{n-1}}{1 + p_{n-1}}, \qquad (2.12)$$

where $q_n^2(a)$ is the gene frequency of an altruistic trait when the population is of age a at the n-th generation, and

$$\frac{\alpha(0,n)}{\beta(0,n)} = \frac{1}{\dfrac{\alpha(0,n)+\beta(0,n)}{\alpha(0,n)}-1} = \frac{1}{\dfrac{1}{q_n^2(0)}-1}$$

$$= \frac{1}{[F(q_{n-1}^2(0))]^{-1}-1}, \qquad (2.13)$$

we have

$$G(p_{n-1}) = \frac{F(\dfrac{p_{n-1}}{1+p_{n-1}})}{1-F(\dfrac{p_{n-1}}{1+p_{n-1}})}, \qquad (2.14)$$

in which F is the fecundity function for q_n^2 defined in Section 3 of Hsieh (1988). If the condition $\hat{\pi}_1(a) > 0$ is imposed as in Hsieh (1988), and

$$-\ln F'(0) < \int_0^1 \hat{\pi}_1(\tau)\, d\tau, \qquad (2.15)$$

(2.14) yields

$$G'(0) = \frac{F'(0)[1-F(0)]-F(0)[-F'(0)]}{[1-F(0)]^2} = F'(0), \qquad (2.16)$$

since $F(0) = 0$, i.e. a population of selfish adults cannot bear altruistic offsprings. The same condition can also be imposed on G. Thus, for $|\theta|$ small, $G(\theta) \cong G'(0)\theta = F'(0)\theta$ and

$$p_n \cong F'(0) \exp[\int_0^1 \hat{\pi}_1(\tau)\, d\tau] p_{n-1}. \qquad (2.17)$$

Relation (2.15) implies that $F'(0) \exp[\int_0^1 \hat{\pi}_1(\tau)d\tau] > 1$ and thus, $p_n > p_{n-1}$ whenever p_{n-1} is sufficiently small. This guarantees that the sequence $\{p_n\}_{n=1}^{\infty}$ will not decrease to 0, and hence, the evolution of an altruist in a population is assured.

III. Analytic Expression for Actual Size of Altruists

From Equation (2.7), we can obtain an expression for the ratio of altruists in the population, given $x_n^0 = x_n(0) = \alpha(0,n), y_n^0 = y_n(0) = \beta(0,n)$:

$$f_n(a) = \frac{x_n(a)}{x_n(a)+y_n(a)} = \frac{x_n^0 \exp[\int_0^a \hat{\pi}_1(\tau)\, d\tau]}{y_n^0 + x_n^0 \exp[\int_0^a \hat{\pi}_1(\tau)\, d\tau]}. \qquad (3.1)$$

Inserting (3.1) into (2.1) yields the following ODE for $x(a)$:

$$x_n'(a) + \phi_{1,n}^{\alpha}(a)x_n(a) + \phi_{2,n}^{\alpha}(a)x_n^2(a) = 0, \qquad (3.2)$$

where

$$\phi_{1,n}^{\alpha}(a) = \pi_1^{\alpha}(a) - \gamma(a)f_n(a) \qquad (3.3)$$

and

$$\phi_{2,n}^{\alpha}(a) = \pi_2(a)/f_n(a). \qquad (3.4)$$

The ODE is valid provided $x_n^0 > 0$, i.e. there are some altruists among the newborns of the generation in question. The solution to the Bernoulli equation in (3.2) is

$$x_n(a) = \frac{x_n^0 \exp[-\int_0^a \phi_{1,n}^{\alpha}(\tau)\, d\tau]}{1 + x_n^0 \int_0^a \phi_{2,n}^{\alpha}(s) \exp[-\int_0^s \phi_{1,n}^{\alpha}(\tau)\, d\tau]\, ds},$$

$$0 \leqslant a \leqslant 1. \qquad (3.5)$$

And from (3.1) and (3.5), we can solve $y(a)$:

$$y_n(a) = \frac{y_n^0 \exp[-\int_0^a \phi_{1,n}^{\beta}(\tau)\, d\tau]}{1 + y_n^0 \int_0^a \phi_{2,n}^{\beta}(s) \exp[-\int_0^s \phi_{1,n}^{\beta}(\tau)\, d\tau]\, ds},$$

$$0 \leqslant a \leqslant 1, \qquad (3.6)$$

where

$$\phi_{1,n}^{\beta}(a) = \pi_1^{\beta}(a) - \gamma(a)f_n(a),$$

$$\phi_{2,n}^{\beta}(a) = \pi_2(a)/[1 - f_n(a)]. \qquad (3.7)$$

Defining the functions $\lambda_1^{\alpha}, \lambda_1^{\beta}, \lambda_2^{\alpha},$ and λ_2^{β} as

$$\lambda_{1,n}^{\alpha}(a) = e^{-\int_0^a \phi_{1,n}^{\alpha}(\tau)\, d\tau}, \quad \lambda_{1,n}^{\beta}(a) = e^{-\int_0^a \phi_{1,n}^{\beta}(\tau)\, d\tau}, \qquad (3.8i)$$

$$\lambda_{2,n}^{\alpha}(a) = \int_0^a \lambda_{1,n}^{\alpha}(\tau)\phi_{2,n}^{\alpha}(\tau)\, d\tau,$$

$$\lambda_{2,n}^{\beta}(a) = \int_0^a \lambda_{1,n}^{\beta}(\tau)\phi_{2,n}^{\beta}(\tau)\, d\tau, \qquad (3.8ii)$$

we have

$$x_n(a) = \frac{x_n^0 \lambda_{1,n}^\alpha(a)}{1 + x_n^0 \lambda_{2,n}^\alpha(a)}, \quad y_n(a) = \frac{y_n^0 \lambda_{1,n}^\beta(a)}{1 + y_n^0 \lambda_{2,n}^\beta(a)}. \tag{3.9}$$

Going back to the notation in Section 1, where $\alpha(a, n + a)$ and $\beta(a, n + a)$ are the altruists and nonaltruists of age a at the n-th generation, (3.9) can be written as

$$\alpha(a, n + a) = \frac{\alpha(0,n) \lambda_{1,n}^\alpha(a)}{1 + \alpha(0,n) \lambda_{2,n}^\alpha(a)}, \tag{3.10}$$

$$\beta(a, n + a) = \frac{\beta(0,n) \lambda_{1,n}^\beta(a)}{1 + \beta(0,n) \lambda_{2,n}^\beta(a)}. \tag{3.11}$$

Assuming that the fecundity function is linear for the altruists, i.e.

$$\alpha(0,n) = F_1(\alpha(1,n)) = \nu \alpha(1,n), \quad \nu > 0, \tag{3.12}$$

the number of adult altruists in the n-th generation just before the (synchronized) reproduction is

$$x_n = \alpha(1,n) = \frac{\lambda_{1,n}^\alpha x_{n-1}}{1 + \lambda_{2,n}^\alpha x_{n-1}}, \tag{3.13}$$

where, using condition imposed on π_2,

$$\lambda_{1,n}^\alpha = \lambda_{1,n}^\alpha(1)\nu > 0, \quad \lambda_{2,n}^\alpha = \lambda_{2,n}^\alpha(1)\nu \geqslant 0. \tag{3.14}$$

Then, for $0 \leqslant m < n$,

$$x_n = H_1^{n,m}(x_m) = \frac{A_{n,m} x_m}{1 + A_{n,m} C_{n,m} x_m}, \tag{3.15}$$

with

$$A_{n,m} = \prod_{j=0}^{n-m-1} \lambda_{1,n-j}^\alpha > 0, \tag{3.16}$$

and

$$C_{n,m} = \sum_{j=0}^{n-m-1} \frac{\lambda_{2,n-j}^\alpha}{\lambda_{1,n}^\alpha \cdots \lambda_{1,n-j}^\alpha} \geqslant 0. \tag{3.17}$$

The scenario is thus strikingly similar to that of a single semelparous population in Coleman and Hsieh (1979), with the exception that the time-dependent functions $\lambda_{1,n}^\alpha$ and $\lambda_{2,n}^\alpha$ vary with the fluctuation of the altruistic ratio $f_n(a)$ in each generation, instead of the environmental factors as in Coleman and Hsieh (1979).

To discuss the asymptotic tendency of the population in question, we let $m \geqslant 0$ be fixed and $x_m > 0$ be given. Using the results given in Coleman and Hsieh (1979), we have the following theorem for the survival of the altruists:

Theorem 1: (i) If $A_{n,m} \to 0$ or $C_{n,m} \to \infty$ as $n \to \infty$, then

$$\lim_{n \to \infty} x_n = 0. \tag{3.18}$$

(ii) Suppose that $0 < \inf_{n > m} C_{n,m} \leqslant \sup_{n > m} C_{n,m} < \infty$, and $A_{n,m} \to \infty$ as $n \to \infty$, then the altruistic members of the population will survive in the sense that

$$\lim_{n \to \infty} [H_1^{n,m}(x_m) - \frac{1}{C_{n,m}}] = 0. \tag{3.19}$$

Moreover, if $\lim_{n \to \infty} C_{n,m}$ exists, then $x_n \to \lim_{n \to \infty} 1/C$ as $n \to \infty$ regardless of the size of the altruists at the m-th generation, x_m.

Making use of equations (3.3), (3.4), and (3.8), we have the following corollary to Theorem 1.

Corollary: If the functions $\hat\pi_1$, π_2 and γ are chosen so that (1) $\phi_{1,n}^\alpha < 0$ in mean, $\forall n > m$, (2) $\infty > \sup_n \lambda_{2,n}^\alpha > 0$, then as $n \to \infty$, $x_n \to$

$$\frac{1}{\lim_{n \to \infty} C_{n,m}} \text{ if the limit exists.}$$

(We define "$\phi_{1,n}^\alpha < 0$ in mean" to satisfy the property $\int_0^1 \phi_{1,n}^\alpha(a) \, da < 0$.)

Similarly, if the fecundity function for the nonaltruists is also linear, i.e. $\beta(0, n) = F_2(\beta(1,n)) = \eta\beta(1,n)$, $\eta > 0$, the corresponding generation growth function for the nonaltruists is

$$y_n = \beta(1,n) = \frac{\lambda_{1,n}^\beta y_{n-1}}{1 + \lambda_{2,n}^\beta y_{n-1}} \tag{3.20}$$

with

$$\lambda_{1,n}^\beta = \lambda_{1,n}^\beta(1)\eta > 0, \quad \lambda_{2,n}^\beta = \lambda_{2,n}^\beta(1)\eta \geqslant 0. \tag{3.21}$$

Subsequently, for $0 \leqslant m < n$,

$$y_n = H_2^{n,m}(y_m) = \frac{B_{n,m} y_m}{1 + B_{n,m} D_{n,m} y_m} \tag{3.22}$$

where

$$B_{n,m} = \prod_{j=0}^{n-m-1} \lambda_{1,n-j}^{\beta} > 0 \qquad (3.23)$$

and

$$D_{n,m} = \sum_{j=0}^{n-m-1} \frac{\lambda_{2,n-j}^{\beta}}{\lambda_{1,n}^{\beta} \cdots \lambda_{1,n-j}^{\beta}} \geqslant 0. \qquad (3.24)$$

Hence, we have a similar theorem for the survival of the nonaltruists:

Theorem 2: If the functions $\hat{\pi}_1$, π_2 and γ are chosen so that (1) $\phi_{1,n}^{\beta} < 0$ in mean, $\forall n > m$, (2) $\infty > \sup_n \lambda_{2,n}^{\beta} > 0$, then $y_n \to \dfrac{1}{\lim\limits_{n \to \infty} D_{n,m}}$ if the limit exists.

If the conditions of both the Corollary and Theorem 2 are satisfied, both the altruists and nonaltruists will coexist in the community. But if, on the other hand, the condition in (i) of Theorem 1 is met, the altruists will become extinct. In fact, we have the following theorem for mutual extinction:

Theorem 3: Suppose (i) $\phi_{1,n}^{\alpha} > 0$ in mean, $\forall n > m$ or $\sup_n \lambda_{2,n}^{\alpha} = \infty$ and (ii) $\phi_{1,n}^{\beta} > 0$ in mean, $\forall n > m$ or $\sup_n \lambda_{2,n}^{\beta} = \infty$, then the whole population will become extinct.

It is important to note that, although the asymptotic behaviour of the altruists and the nonaltruists depends on different sets of parameters, the parameters $\phi_{1,n}^{\alpha}$, $\phi_{1,n}^{\beta}$, $\phi_{2,n}^{\alpha}$, $\phi_{2,n}^{\beta}$ are related by the simple fact that they are given in terms of the altruistic ratio of age a at the n-th generation, $f_n(a)$, as defined in (3.3), (3.4) and (3.7). Thus, the fates of the altruists and the nonaltruists are strongly bonded. To illustrate the point, let us consider the example where $\hat{\pi}_1(a) < 0$, $0 \leqslant a \leqslant 1$, with $\lambda_{1,n}^{\beta} > \lambda_{1,n}^{\alpha}$ in mean, $\forall n > m$, and $f_n(1) \to 0$ as $n \to \infty$. In this case, $x_n \to 0$ as $n \to \infty$ no matter how we choose the functions $\hat{\pi}_1$, π_2, and γ, since

$$\phi_{2,n}^{\alpha} = \frac{\pi_2(a)}{f_n(a)} \quad \text{and} \quad \sup_n \lambda_{2,n}^{\alpha} = \infty. \qquad (3.25)$$

Hence, the survival of an altruistic community still depends on the "relative" size of the functions π_1^{α} and π_1^{β} as shown in Hsieh (1988).

IV. Conclusions and Examples

In many biological populations, a phenomenon could occur where a group of altruists suddenly migrates into a community of strictly selfish individuals, or vice versa. In such an instance, the survival of the altruist becomes questionable. In our model, this possibility is taken into account in the functions π_1^{α} and π_1^{β}, since they account for the effects of mortality and migration on a population. Equations (3.15)-(3.17) and Theorem 1 in the previous section imply that if a community with no altruist is suddenly invaded by a group of altruists at time $t = m$ (hence $x_m = \alpha(1,m) > 0$), the number of altruists in the community will converge to $1/\lim_{n \to \infty} C_{n,m}$ provided the conditions in Corollary are met, i.e. the altruists will survive no matter how small the initial group of altruists is. Ditto for the case of nonaltruists invading an altruistic society, as long as conditions in Theorem 2 are met.

Nevertheless, survival of altruists in a community is not altogether the same as the evolution of altruism. In Hsieh (1988), we have shown that $\int_0^1 \hat{\pi}_1(a) \, da > -\ln F'(0)$ implies the evolution of altruism in the sense that the gene frequency q_n^{λ} becomes fixed as $n \to \infty$. However, this condition does not guarantee the survival of altruists. For, in the case of Theorem 3, both x_n and y_n go to zero as $n \to \infty$, and yet, it is possible for the ratio of altruists to remain nonzero for all time if the numbers of both altruists and nonaltruists are decreasing at the same rate. The above possibility is illustrated with simulated examples.

For the simulated populations, we let $\pi_2(a) = \gamma(a) = a$, $\nu = \eta = 1$, and use the initial condition of $\alpha(0,0) = 1$, $\beta(0,0) = 1.5$. For the first simulation run, we let $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = -a$ so that the evolution of altruism is assured as well as the survival of altruists. The graph of adult population size *vs* generation is given in Fig. 1 where, after 15 generations, the number of adult altruists converges to 0.410 while the nonaltruistic adults total 0.629. In other words, if we start with 1000 altruists and 1500 nonaltruists, the respective numbers will become fixed at 410 and 629 after approximately 15 generations. Moreover, the gene frequency will also become stable at 0.628 (see Fig. 2). But if we let $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = a$, the gene frequency is still fixed at 0.626 (Fig. 4), but both the altruists and nonaltruists will become extinct (see Fig. 3).

Since π_1^{α} and π_1^{β} denote the effects of mortality and migration on the altruists and nonaltruists, respectively, the case of Figs. 1 and 2, where π_1^{α} and π_1^{β} are negative, could be interpreted as having a large flow of immigrants which helps maintain the stability of the population. However, if the net migration is only minor compared to mortality as in the case of Figs. 3 and 4, the population will become extinct even if the ratio of altruists in the population is fixed throughout the demise of the community.
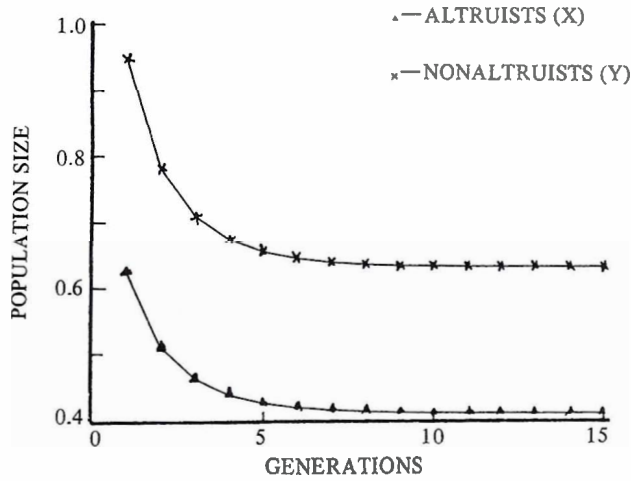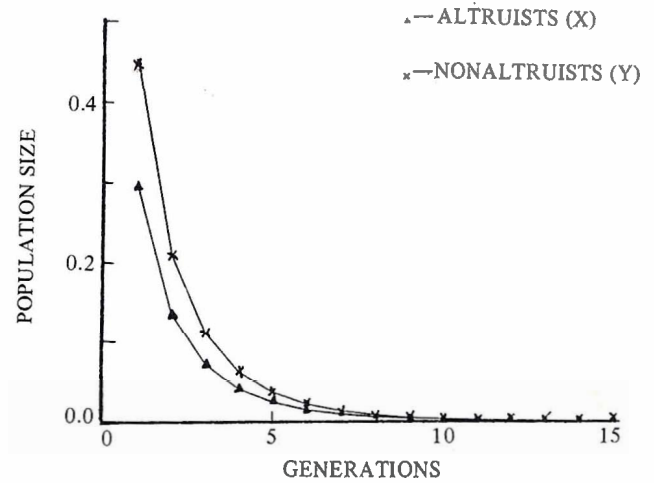
Acknowledgement

Fig. 1. Population sizes of adult altruists and nonaltruists at the n-th generation for $n = 1, \ldots, 15$ with $\pi_2(a) = \gamma(a) = a$, $\nu = \eta = 1$ $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = -a$.

Fig. 3. Population sizes of adult altruists and nonaltruists at the n-th generation for $n = 1, \ldots, 15$ with $\pi_2(a) = \gamma(a) = a$, $\nu = \eta = 1$, $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = a$.
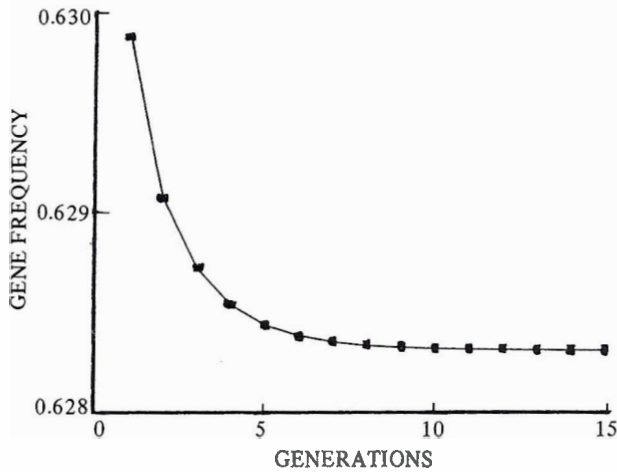

Fig. 2. Gene frequency $q_n(1)$ of adult altruists of the n-th generation for $n = 1, \ldots, 15$ with $\pi_2(a) = \gamma(a) = a$, $\nu = \eta = 1$, $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = -a$.
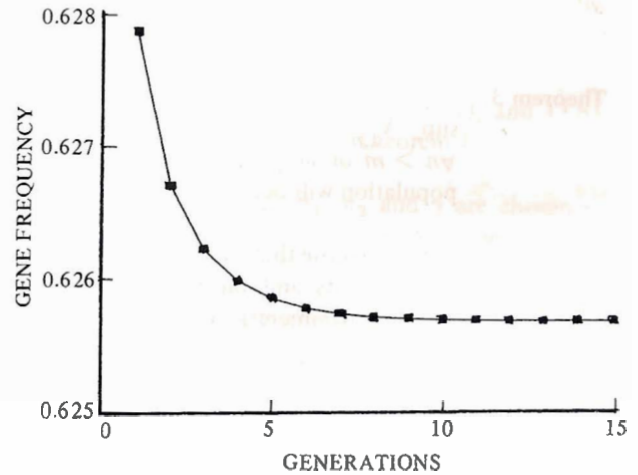

Fig. 4. Gene frequency $q_n(1)$ of adult altruists of the n-th generation for $n = 1, \ldots, 15$ with $\pi_2(a) = \gamma(a) = a$, $\nu = \eta = 1$, $\pi_1^{\alpha}(a) = \pi_1^{\beta}(a) = a$.

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利它棲群在平等受益時之演化及延續

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摘 要

本文以微分方程式來探討利它棲群在平等受益之情況下的演化條件。我們將求得利它基因頻率 $f_n(a)$ 之公式及在棲群中利它個體及非利它個體之數量,並舉例證明利它行為之演化並不保證利它棲群之延續。