mathematical population dynamics

dynamics

proceedings of the second international conference

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Lecture Notes in Pure and Applied Math., V. 131

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Altruistic Population Model with Sex Differences

YING-HEN HSIEH

National Chung-Hsing University, Taichung, Taiwan, Republic of China

I. INTRODUCTION

The evolution of altruism in ecosystems is an intriguing phenomenon in biology. We define "evolution" as having a fixed ratio of the population showing one particular characteristic, such as performing altruistic acts. The problem is interesting and complicated because (1) the evolution of a self-sacrificing subpopulation seems to be a direct contradiction to the theory of evolution — the altruistic acts usually decreases an individual's fitness to survive, and (2) the altruistic act performed can be, at times, age-dependent, sex-dependent, space-dependent, or group-dependent. The literature on altruism includes Hamilton (1964), Maynard Smith (1965, 1980), Trivers (1971), Cavalli-Sforza and Feldman (1978), Feldman and Cavalli-Sforza (1981), and Akin (1984).

Population geneticists in general believe that altruism was able to evolve in a community due to one of the three factors: reciprocal altruism, kin selection, or group selection (see Akin, 1984), but the relative importance of these three factors is still very much in controversy. The purpose of this work is not to ask why altruism evolves, but how. We will use simple mathematical models to find the circumstances under which altruism is able to evolve in certain communities but not in others. It is easy to foresee that the conditions will be both physiological and environmental.

In previous works by the author (Hsieh, 1988, 1989a), a model of coupled Von Foerster equations of the form

$$Dx(a, t) + \alpha_1(\alpha)x(a, t) + \pi_1(a)x(a, t)[x(a, t) + y(a, t)]$$
$$- \frac{\gamma_1(a)x^2(a, t)}{x(a, t) + y(a, t)} = 0 \tag{1}$$

$$Dy(a, t) + \alpha_2(a)y(a, t) + \pi_2(a)y(a, t)[x(a, t) + y(a, t)]$$
$$- \frac{\gamma_2(a)y(a, t)x(a, t)}{x(a, t) + y(a, t)} = 0, \qquad t \le 0, \quad a \in [0, 1] \tag{2}$$

was used to study the possibility of evolution of altruism in a community with the numbers of altruistic and selfish individuals represented by separate differential equations. [For a discussion on models of this type, see Coleman (1978).] The conditions for the persistence of the altruistic group in the population was obtained under the assumption of synchronized reproduction in a semelparous population where reproduction occurs once in each individual's lifetime. In a subsequent work (Hsieh, 1989b), it was also shown that under the assumption of indiscriminate altruism for all individuals in the community, the evolution of altruism is necessary but not sufficient for the persistence of the community itself.

The Von Foerster equation is generally associated with one-sex models where only the female members of the population are considered. However, in some altruistic communities with intricate structure such as social insects, there is usually a difference in the performance of altruistic act between male and female, as well as different reproductive rates for each sex. One example is the social bees (honeybees and bumblebees), where different forms of altruistic acts are performed by the (adult) male and female of the species in a complex social structure. Headed by the queen bee, whose sole function is to lay eggs (up to 2000 a day), the community is comprised of female workers, which build cells for the eggs and collect enough pollen to feed the larva until it becomes a flying adult bee; male bees, which fertilize the young queens; and the parasitic (nonaltruistic) bees, which do not build hives and develop in the cells of the host working bees.

In Hsieh (1988), we get around this problem by prescribing a fecundity function that is general enough to account for the discrepancy in the sex ratio of succeeding generations. But to deal with the different levels of altruism, we introduce separate equations for the male and female members of the altruistic group so that distinct altruistic functions and fecundity functions can be assigned accordingly to different sex groups. However, we will not distinguish sex among the selfish members of the community since both sexes benefit equally from altruistic acts. Therefore, not only is the difference in ability to perform altruistic act considered, but we can also take into account the possible change in sex ratio from generation to generation. The model in question is as follows:

$$Dx(a, t) + \alpha_1(a)x(a, t) + \pi_1(a)x(a, t)N(a, t)$$
$$- \frac{\gamma_1(a)x(a, t)[x(a, t) + y(a, t)]}{N(a, t)} = 0 \tag{3}$$

$$Dy(a, t) + \alpha_2(a)y(a, t) + \pi_2(a)y(a, t)N(a, t)$$
$$- \frac{\gamma_2(a)y(a, t)[x(a, t) + y(a, t)]}{N(a, t)} = 0 \tag{4}$$

$$Dy(a, t) + \alpha_3(a)z(a, t) + \pi_3(a)z(a, t)N(a, t)$$
$$- \frac{\gamma_3(a)z(a, t)[x(a, t) + y(a, t)]}{N(a, t)} = 0, \qquad t \leq 0, \quad a \in [0,1] \tag{5}$$

x, y, z denotes the number of male altruists, female altruists, and nonaltruists, respectively, and $N = x + y + z$ is the total population.

In Section II we reduce the equations (3)–(5) into a simpler system for the altruistic ratio so that in Section III we can yield analytical results on sufficient

conditions for a fixed sex ratio in the altruistic group. Finally, we will run computer simulations for different cases described previously in the text and discuss the biological and ecological implications of our results.

Although the main theme is sex differences in altruistic acts, the model can be used to describe any situations where any three subgroups of a population performing distinct social behavior (not necessary altruism). It also allows different levels of mortality and reproduction for each subgroups. Hence the analysis could have wider application in studying the complicated communities of semelparous insects.

II. MODEL FOR ALTRUISTIC RATIO

Let $X_n(a)$, $Y_n(a)$, $Z_n(a)$ be the numbers of altruistic males, altruistic females, and selfish individuals, respectively, of age a at the nth generation. By the assumption of semelparous population with synchronized reproduction, equations (3)–(5) can be simplified (see Coleman, 1978, or Coleman and Hsieh, 1979) as follows:

$$X_n'(a) + \alpha_1(a)X_n(a) + \pi_1(a)X_n(a)N_n(a)$$
$$- \gamma_1(a)\frac{X_n(a) + Y_n(a)}{N_n(a)}X_n(a) = 0 \tag{6a}$$

$$Y_n'(a) + \alpha_2(a)Y_n(a) + \pi_2(a)Y_n(a)N_n(a)$$
$$- \gamma_2(a)\frac{X_n(a) + Y_n(a)}{N_n(a)}Y_n(a) = 0 \tag{6b}$$

$$Z_n'(a) + \alpha_3(a)Z_n(a) + \pi_3(a)Z_n(a)N_n(a)$$
$$- \gamma_3(a)\frac{X_n(a) + Y_n(a)}{N_n(a)}Z_n(a) = 0, \qquad 0 \le a \le 1 \tag{6c}$$

Here $N_n(a) = X_n(a) + Y_n(a) + Z_n(a)$ is the total population number of the nth generation at age a, the α_i's are mortality functions, the π_i's denote the effect of dispersal and migration, the γ_i's are "altruistic functions" from $[0, 1] \rightarrow R$ which describe the effects of altruism on each group (hence a group that incurs a loss in fitness due to altruism performed may have a negative altruistic function), and the generation length is normalized to unity.

We assume further that the rate of dispersal and migration is the same for all groups (i.e., $\pi_1 = \pi_2 = \pi_3$). If we let

$$f_n(a) = \frac{X_n(a) + Y_n(a)}{N_n(a)} \tag{7}$$

be the altruistic ratio in the nth generation of age a and

$$g_n(a) = \frac{Y_n(a)}{X_n(a) + Y_n(a)} \tag{8}$$

be the ratio of females among the altruists of the nth generation and age a, we can combine (6a)–(6c) to get the corresponding equations satisfied by $f_n(a)$ and $g_n(a)$ for $0 \le a \le 1$ and $n \in Z$:

$$f_n'(a) - f_n(a)[1 - f_n(a)][\hat{\alpha}_1(a) - \hat{\alpha}_2(a)g_n(a)$$
$$+ \hat{\gamma}_1(a)g_n(a)f_n(a) - \hat{\gamma}_2(a)f_n(a)] = 0 \tag{9a}$$

$$g_n'(a) + g_n(a)[1 - g_n(a)][\hat{\alpha}_2(a) - \hat{\gamma}_2(a)f_n(a)] = 0 \tag{9b}$$

with

$$\hat{\alpha}_1(a) = \alpha_3(a) - \alpha_1(a) \tag{10}$$

$$\hat{\alpha}_2(a) = \alpha_2(a) - \alpha_1(a) \tag{11}$$

$$\hat{\gamma}_1(a) = \gamma_3(a) - \gamma_1(a) \tag{12}$$

$$\hat{\gamma}_2(a) = \gamma_2(a) - \gamma_1(a) \tag{13}$$

To equations (9), we add the fecundity functions F_1 and F_2 for the altruistic ratio and the ratio of females within the altruistic group, respectively,

$$f_{n+1}(0) = F_1(f_n(1)) \tag{14a}$$
$$g_{n+1}(0) = F_2(g_n(1)) \tag{14b}$$

The role of female reproduction as an altruistic act does not appear, although it certainly qualifies as altruism. However, a consideration of female reproduction can be incorporated into the altruistic function for female altruists; hence the females classified in the selfish group are those females that do not perform altruistic tasks and reproduce no offsprings. We can then look for sufficient conditions for the evolution of altruism as well as a fixed ratio of female altruists in the population using the fixed-point theory developed by Coffman and Coleman (1978).

III. ANALYSIS OF THE MODEL

Equations (9) can be rewritten as

$$f_n'(a) + \rho_1(f_n(a), g_n(a), a) = 0 \tag{15a}$$
$$g_n'(a) + \rho_2(f_n(a), g_n(a), a) = 0, \qquad 0 \le a \le 1, \quad n \in Z \tag{15b}$$

where

$$\rho_1(x, y, a) = -x(1 - x)[\hat{\alpha}_1(a) - \hat{\alpha}_2(a)y + \hat{\gamma}_1(a)xy - \hat{\gamma}_2(a)x] \tag{16a}$$
$$\rho_2(x, y, a) = y(1 - y)[\hat{\alpha}_2(a) - \hat{\gamma}_2(a)x] \tag{16b}$$

are the loss functions for f_n and g_n.

Since the conditions for evolution of altruism were given in Hsieh (1988), the first question we pose is the following: Suppose that the altruistic ratio for adults at each generation $f_n(1)$ becomes fixed and positive at each generation as $n \to \infty$. What is the ratio of female altruists in the altruistic group?

If we defined the generation growth function G: $[0, 1] \to [0, 1]$ for the adult female ratio among altruists $g_n(1)$ as follows:

$$g_n(1) = G(g_{n-1}(1)), \qquad n \in Z \tag{17}$$

where the initial value $g_n(0)$ of the IVP (15b) is given by (14b), the conditions for

the existence of a fixed point of (17) are given as follows:

Theorem 1. Suppose that $0 < \lim_{n \to \infty} f_n(1) < 1$ and $\partial^2 \rho_2 / \partial y^2 \geq 0$ for each $a \in [0, 1]$, $x, y \in [0, 1]$. If

(a) $F_2(0) > 0$

or

(b) $\ln F_2'(0) > \int_0^1 [\hat{\alpha}_2(a) + |\hat{\gamma}_2(a)|] \, da$

there exists a unique fixed positive point $\hat{g} = G(\hat{g})$. If, on the other hand, $F_2(0) = 0$ and

$$\ln F_2'(0) < \int_0^1 [\hat{\alpha}_2(a) - |\hat{\gamma}_2(a)|] \, da \tag{18}$$

every solution of (17) goes to 0 as $n \to \infty$ (i.e., 0 is the unique fixed point).

This theorem is an obvious consequence of the result of the last example given in Coffman and Coleman (1978). The assumpion of evolution of altruism in Theorem 1 is most relevant, since without it the convergence to a fixed sex ratio in the altruistic group could be meaningless, as we demonstrate with a numerical example at the end of this chapter.

From (16) we have

$$\frac{\partial^2 \rho_2}{\partial y^2} = -2[\hat{\alpha}_2(a) - \hat{\gamma}_2(a)x] \tag{19}$$

Hence, if

$$\hat{\alpha}_2(a) \leq \min\{0, \hat{\gamma}_2(a)\}, \qquad a \in [0, 1] \tag{20}$$

the convexity condition on ρ_2 in Theorem 1 is satisfied.

Since $g_n(0)$ denotes the ratio of females among the newborn altruists, it is safe to assume that the ratio is more or less approximately 1/2. So if we let $F_2(y) = 1/2$, the persistence of female altruists is guaranteed as long as altruism evolves and condition (20) is satisfied.

From (16) we get

$$\frac{\partial^2 \rho_1}{\partial x^2} = 2[\hat{\gamma}_1(a)y - \hat{\gamma}_2(a)](3x - 1) + 2[\hat{\alpha}_1(a) - \hat{\alpha}_2(a)y] \tag{21}$$

The convexity condition on ρ_1 requires that for $a \in [0, 1]$,

$$\hat{\alpha}_1(a) \geq \max\{0, \hat{\alpha}_2(a)\} \tag{22}$$

$$\hat{\alpha}_1(a) + \hat{\gamma}_2(a) \geq \max\{0, \hat{\alpha}_2(a) + \hat{\gamma}_1(a)\} \tag{23}$$

$$\hat{\alpha}_1(a) + 2\hat{\gamma}_2(a) \geq \max\{0, \hat{\alpha}_2(a) - 2\hat{\gamma}_1(a)\} \tag{24}$$

Thus we have a theorem for evolution of altruism with fixed ratio of female altruists as follows:

Theorem 2. Let $\hat{\alpha}_1$, $\hat{\alpha}_2$, $\hat{\gamma}_1$, $\hat{\gamma}_2$ satisfy the inequalities in (20) and (22)–(24). If the fecundity functions F_i satisfies either

(a) $F_i(0) > 0$ for $i = 1, 2$

or

(b) $\ln F_1'(0) > \int_0^1 \hat{\alpha}_1(a) \, da$

and

(b') $\ln F_2'(0) > \int_0^1 [\hat{\alpha}_2(a) + |\hat{\gamma}_2(a)|] \, da$

altruism will evolve with a fixed ratio of female altruists in the altruistic group.

Conditions (22)–(24) together with (a) or (b) and (b') in Theorem 2 give sufficient conditions for evolution of altruism in a population model with sex differences. We will now compare these conditions with the corresponding results for a one-sex model. We recall that the convexity conditions for evolution of altruism in a one-sex model (Hsieh, 1988) are

$$\hat{\pi}_1(a) \geq 0 \tag{25}$$

and

$$\frac{\hat{\pi}_1(a)}{2} > \hat{\gamma}(a) > - \hat{\pi}_1(a), \qquad a \in [0, 1] \tag{26}$$

where

$$\hat{\pi}_1(a) = \pi_1^\beta(a) - \pi_1^\alpha(a) \tag{27}$$

is the difference in mortality of selfish group (π_1^β) and altruists (π_1^α), and

$$\hat{\gamma}(a) = \gamma_\beta(a) - \gamma_\alpha(a) \tag{28}$$

is the difference in altruistic functions for the selfish members (γ_β) and for altruists (γ_α).

Condition (25) says that the mortality function of altruists must be no worse than that of selfish group at any time. We note that (22) implies

$$\alpha_3(a) \geq \max\{\alpha_1(a), \alpha_2(a)\}, \qquad a \in [0, 1] \tag{29}$$

which means the mortality rate of the selfish group is no lower than either the male or female altruists at any time — exactly what we have in (25).

Conditions (23) and (24) can be rewritten respectively as

$$\hat{\gamma}_2(a) \geq \max\{-\hat{\alpha}_1(a), \hat{\alpha}_2(a) - \hat{\alpha}_1(a) + \hat{\gamma}_1(a)\} \tag{30}$$

and

$$-2\hat{\gamma}_2(a) \geq \max\{-\hat{\alpha}_1(a), \hat{\alpha}_2(a) - \hat{\alpha}_1(a) - 2\hat{\gamma}_1(a)\}, \qquad a \in [0, 1] \tag{31}$$

Hence if $\hat{\gamma}_2(a) = \hat{\alpha}_2(a) = 0$, $a \in [0, 1]$ (i.e. we do not distinguish sex among the altruists), then (30) and (31) together imply that

$$\hat{\alpha}_1(a) \geq \hat{\gamma}_1(a) \geq - \tfrac{1}{2}\hat{\alpha}_1(a), \qquad a \in [0, 1] \tag{32}$$

which is different from (26). It is quite reasonable, since evolution of altruism with a nonzero fixed female altruistic ratio is not altogether the same as evolution of altruism per se. But it is interesting that condition (32), although different from (26), has the similar implication that the net altruistic benefit, whether negative or not, should be of moderate magnitude for altruism to evolve. Thus the moral lesson is: There must be a certain balance in nature!

As a final remark before we get to numerical examples, it is interesting to note that when $\hat{\gamma}_1(a) = \hat{\alpha}_2(a) = 0$, (30) and (31) yield

$$\frac{\hat{\alpha}_1(a)}{2} \geq \hat{\gamma}_2(a) \geq -\hat{\alpha}_1(a) \tag{33}$$

which is exactly condition (26).

One possible interpretation of condition (33) is that when the whole altruistic group has the same mortality function, which is no greater than that of the selfish group but the male altruists benefit as much from altruistic acts as the selfish group, the female altruists can still persist whether or not they are benefitted more from the altruistic acts than the male altruists — as long as the total difference in fitness incurred is of moderate magnitude. In fact, if we interchange sex roles (let X_n denote females and Y_n denote males), we then have a situation where male altruists, although possibly making a greater sacrifice in their altruism, will still evolve. Hence the model allows us to study altruistic communities without prejudging which of the three groups is making the greater overall sacrifice.
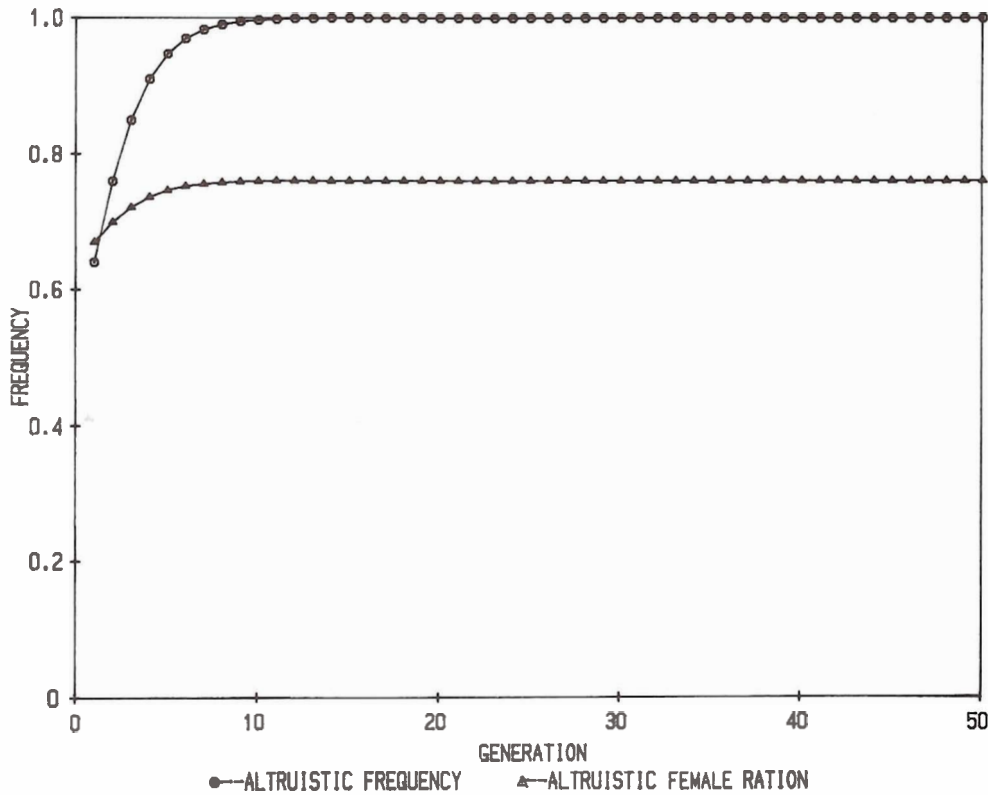

Figure 1 Altruistic frequency $f_n(1)$ (circles) and fraction of female altruists $g_n(1)$ (triangles) at adulthood with $f_0(0) = g_0(0) = 1/2$; $F_1(x) = x$, $F_2(y) = 1/2$, $\hat{\alpha}_1(a) = a$, $\hat{\alpha}_2(a) = -a/5$, $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = a/10$.

IV. EXAMPLES AND DISCUSSION

In this section we use simulated numerical examples to illustrate our results. In all cases, we use a fourth-order Runge–Kutta method with $h = 0.05$ to solve $f_n(1)$ and $g_n(1)$ for $n = 1, 2, 3, \ldots$, using equations (9a) and (9b) simultaneously. We also use the initial values of $f_0(0) = g_0(0) = 0.5$ for all simulations. In Fig. 1 we let $F_1(x) = x$, $F_2(y) = 1/2$ (i.e., the altruistic group is equally divided between males and females), $\hat{\alpha}_1(a) = a$, $\hat{\alpha}_2(a) = -a/5$, $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = a/10$, so that the functions satisfy the conditions in Theorem 2. As we can see from Fig. 1, the community approaches a pure altruistic society with a female ratio of 0.7088. A simple biological explanation for condition (20) is: For female altruists to evolve, it is sufficient that they be more competitive physiologically $[\alpha_2(a) < \alpha_1(a)]$ and that this competitive edge outweighs the edge that male altruists have as beneficiaries of altruistic acts, if, indeed, the males have such an edge $[\gamma_2(a) < \gamma_1(a)]$.

The convexity condition in Theorem 1 is sufficient but not necessary, as we shall demonstrate in the next example. For Fig. 2 we let $F_1(x) = x$ and $F_2(y) = 1/2$ as before, but we let $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = -a$, $\hat{\alpha}_1(a) = \hat{\alpha}_2(a) = -a/5$. The functions prescribed here do not satisfy either condition (20) or the convexity condition in
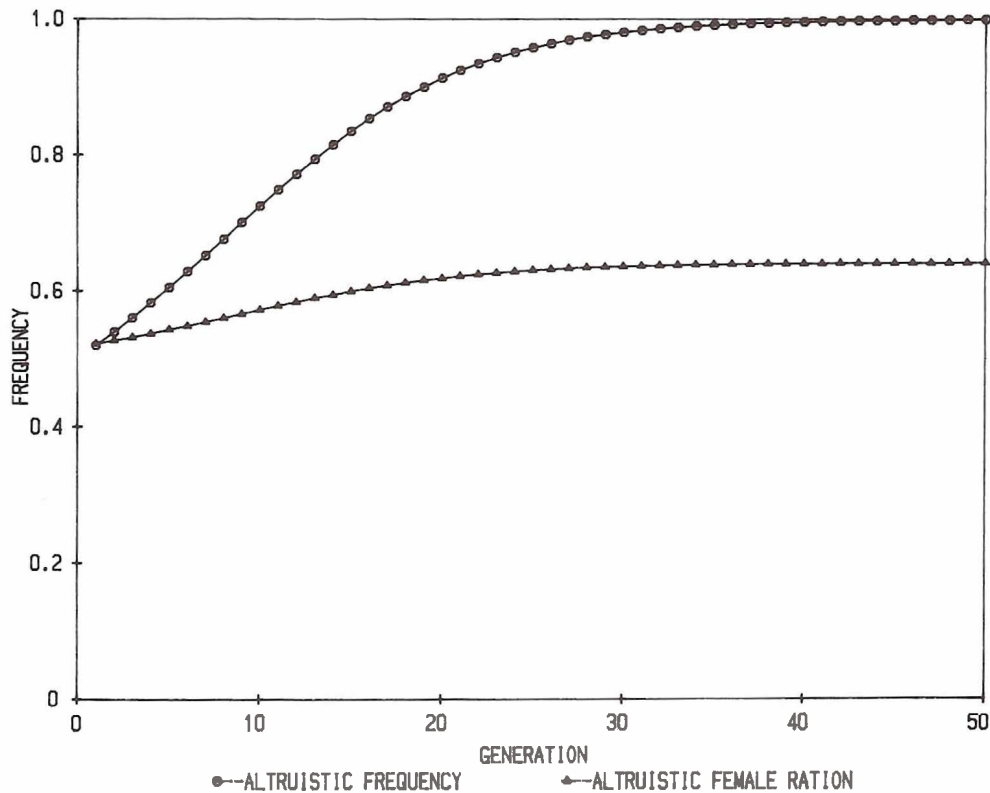

Figure 2   Altruistic frequency $f_n(1)$ (circles) and fraction of female altruists $g_n(1)$ (triangles) at adulthood with $f_0(0) = g_0(0) = 1/2$; $F_1(x) = x, F_2(y) = 1/2$, $\hat{\alpha}_1(a) = \hat{\alpha}_2(a) = -a/5$, $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = -a$.
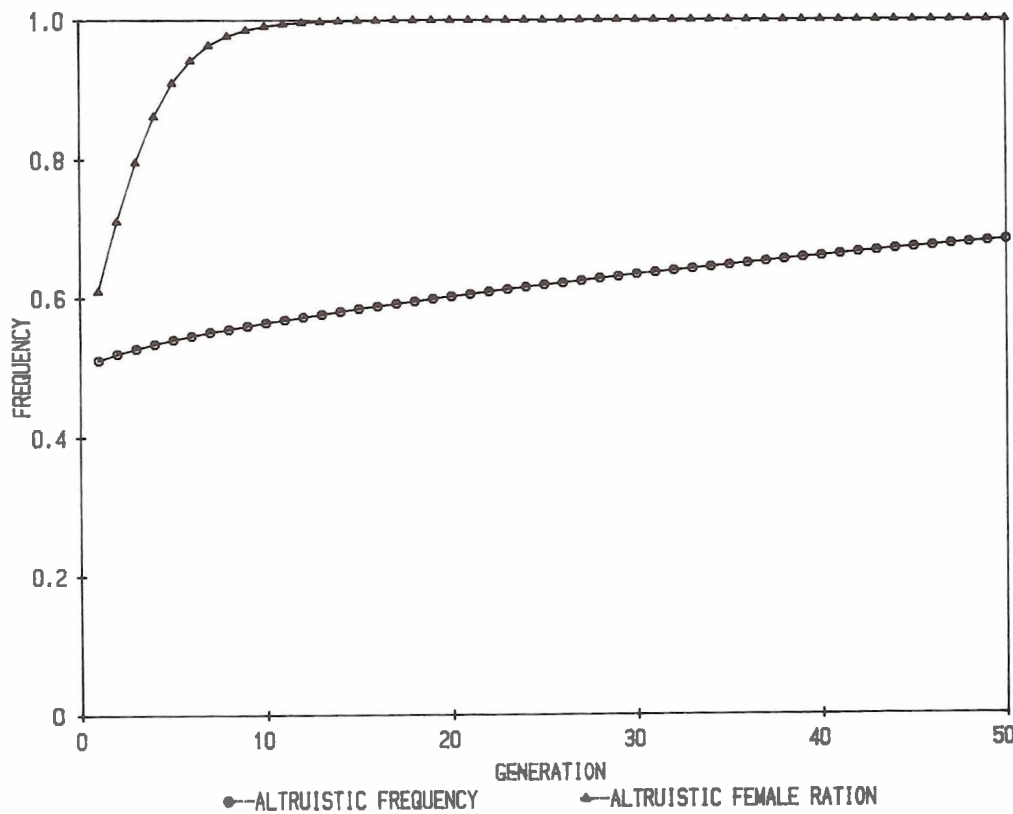
Figure 3 Altruistic frequency $f_n(1)$ (circles) and fraction of female altruists $g_n(1)$ (triangles) at adulthood with $f_0(0) = g_0(0) = 1/2$; $F_1(x) = x$, $F_2(y) = y$, $\hat{\alpha}_1(a) = a/5$, $\hat{\alpha}_2(a) = a/10$, $\hat{\gamma}_1(a) = a/10$, $\hat{\gamma}_2(a) = (1 - 2a)/5$.

Theorem 1, but as one can see from Fig. 2, we still have evolution of pure altruism in the population with a fixed female ratio of 0.6410 as $n \to \infty$.

The most interesting case in nature could be the instances where altruism evolves in a community with the altruistic act performed by solely one sex (male or female). The following example illustrates that such a phenomenon is possible in our model. In Fig. 3 we let $F_1(x) = x$, $F_2(y) = y$, $\hat{\alpha}_1(a) = a/5$, $\hat{\alpha}_2(a) = a/10$, $\hat{\gamma}_1(a) = a/10$, $\hat{\gamma}_2(a) = (1 - 2a)/5$. (The given fecundity function F_2 is probably not very realistic biologically, but is nonetheless possible.) Then altruism will evolve with an all-female altruistic group. One example with all-male altruistic group could easily be obtained by interchanging $X_n(a)$ and $Y_n(a)$ in the original model in (6).

In conclusion we point out that it is possible for $g_n(1)$ to converge to a nonzero fixed point without evolution of altruism. For Fig. 4 we let $F_1(x) = x$, $F_2(y) = y$, $\hat{\alpha}_1(a) = -a$, $\hat{\alpha}_2(a) = -a/5$, and $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = a/10$; then the altruistic group will eventually consist solely of females, but the altruistic ratio will go to zero. So in reality, the number of female altruists will also go to zero and the altruists become
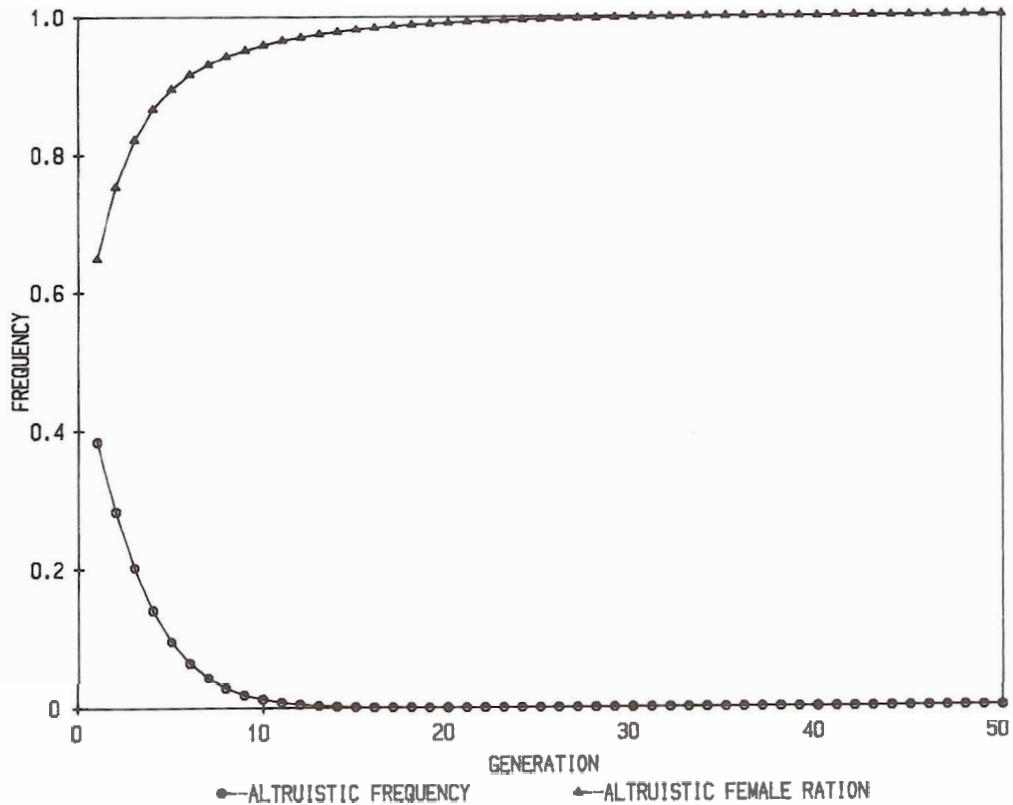
Figure 4   Altruistic frequency $f_n(1)$ (circles) and fraction of female altruists $g_n(1)$ (triangles) at adulthood with $f_0(0) = g_0(0) = 1/2$; $F_1(x) = x$, $F_2(y) = y$, $\hat{\alpha}_1(a) = -a$, $\hat{\alpha}_2(a) = -a/5$, $\hat{\gamma}_1(a) = \hat{\gamma}_2(a) = a/10$.

extinct. Hence a fixed ratio of female altruists is only meaningful given that altruism will persist.

ACKNOWLEDGMENTS

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