

EVOLUTION OF ALTRUISTIC COMMUNITIES¹

Ying-Hen Hsieh, Department of Applied Mathematics, National Chung-Hsing University, Taichung, Taiwan

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Abstract. An age-dependent model which examines the factors determining the evolution of altruism in a community is proposed, and a theorem which yields precise conditions for the evolution of altruistic community and for the extinction of altruistic individuals in a population is given. The ecological significance of the conditions is discussed, together with some mathematical details. Simulated examples to illustrate the analytical results are also presented.

Introduction

The question of evolution of altruism in ecosystems has long been a topic of interest among population biologists. A partial list of 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). The question is interesting because the act of altruism is an action of interacting individuals (sometimes of different species) which occurs in many species of insects and animals, and yet is hard to describe in terms of simple mathematical models. It is also an intricate phenomenon of nature which at times can be age-dependent, sex-dependent, space-dependent, group-dependent, any combination of the above.

Recently, I proposed a model of coupled Von Foerster equations to study the evolution of altruistic communities with age-dependent altruism (Hsieh 1988). Assuming semelparous population (which is common in insect species) of fixed generation length (normalized to unity), the equation can be simplified as follows:

$$x'_n(a) + \pi_1^\alpha(a) x_n(a) + \pi_2(a) x_n(a) [x_n(a) + y_n(a)] - \gamma_\alpha(a) \frac{x_n(a)}{x_n(a) + y_n(a)} x_n(a) = 0, \quad (1.1)$$

$$y'_n(a) + \pi_1^\beta(a) y_n(a) + \pi_2(a) y_n(a) [x_n(a) + y_n(a)] - \gamma_\beta(a) \frac{y_n(a)}{x_n(a) + y_n(a)} y_n(a) = 0, 0 \leq a \leq 1. \quad (1.2)$$

Here $x_n(a)$, $y_n(a)$ are the numbers of altruists and non-altruists of age a , respectively, in the population at the n th generation. The functions π_1^α , π_1^β , and π_2 describe the effects of mortality and migration (which are seasonal), while γ_α and γ_β are the altruistic functions (which are age-dependent). Therefore, these functions

do not alter from generation to generation. However, an extension of the model in which the above functions do vary with each generation can be easily obtained without affecting the analytical results (see Coleman and Hsieh 1979, Hsieh 1989).

Hsieh (1988) showed that under certain convexity conditions on π_1^α , π_1^β , γ_α , and γ_β , and given restrictions on the reproductive rate, any population with at least some altruists in the population at any given time will evolve into an altruistic society in the sense that the ratio of altruists in the population will remain fixed and nonzero. Furthermore, under the additional assumption of indiscriminate altruism ($\gamma_\alpha = \gamma_\beta$), evolution of altruism is necessary for the persistence of the community but not sufficient to guarantee its survival (Hsieh 1989).

A more precise theorem on the evolution of altruistic community, together with a discussion of the ecological significance of the conditions on the fecundity function, is given. It is also shown that the restrictions imposed on the reproductive rate is general enough to include cases where the altruistic trait is genetically recessive. Finally, I demonstrate that some of the conditions imposed on γ_α and γ_β are mainly for mathematical convenience and do not effect the overall results.

The effect of reproductive rate

In Hsieh (1988), equations (1.1) and (1.2) were reduced to a single equation:

$$f'_n(a) - \hat{\pi}_1(a) f_n(a) + [\hat{\pi}_1(a) + \hat{\gamma}(a)] f_n^2(a) - \hat{\gamma}(a) f_n^3(a) = 0, \quad (2.1)$$

where $f_n(a) = x_n(a)/[x_n(a) + y_n(a)]$ is the altruistic ratio of the n th generation at age a , $\hat{\pi}_1(a) = \pi_1^\alpha(a) - \pi_1^\beta(a)$, and $\hat{\gamma}(a) = \gamma_\beta(a) - \gamma_\alpha(a)$. The fecundity function F for the altruistic ratio of succeeding generations

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is prescribed by

$$\hat{f}_n(0) = F(f_{n-1}(1)) \tag{2.2}$$

Making use of the qualitative theory in Coffman and Coleman (1978), the following theorem can be obtained:

Theorem:

Let $\hat{\gamma}$ be continuous on $[0, 1]$ and let $\hat{\pi}_1$ be continuous and positive on $[0, 1]$ with $\hat{\pi}_1(a)/2 \geq \hat{\gamma}(a) \geq -\hat{\pi}_1(a)$, $a \in [0, 1]$. If either
 (i) $\ln F'(0) > -\int_0^1 \hat{\pi}_1(a) da$
 or (ii) $F'(0) (>) 0$ and $\ln F'(0) \leq -\int_0^1 \hat{\pi}_1(a) da$,
 the altruistic ratio $f_n(0)$ at the beginning of each generation will become fixed and nonzero. On the other hand, if
 (a) $F'(0) = 0$
 and (b) $\ln F'(0) < -\int_0^1 \hat{\pi}_1(a) da$,
 $f_n(0) = 0$ is globally stable, i.e. the altruistic members will become extinct.

The continuity condition on $\hat{\gamma}$ is due to a theorem by Hartman (1964, Theorem 3.1, Chapter 5) but can actually be weakened a bit. An example of such will be given at the end of the next section.

The significance of the conditions on $\hat{\pi}_1$ and $\hat{\gamma}$ was discussed in Hsieh (1988). Moreover, it is much more appropriate in terms of ecological interpretations. Condition (b) for extinction places an upper bound on the rate of increase of the fecundity function when the altruistic ratio is small, while condition (a) implies that nonaltruists cannot bear altruistic offsprings. In other words, if only altruistic parents beget altruistic offspring and the altruistic ratio cannot undergo drastic increase through reproduction when the altruists are few in number, they will eventually be wiped out of the population. On the other hand, if the increase in reproduction of altruistic offsprings is large enough in the neighborhood of a very small altruistic ratio so that $\ln F'(0) (>) -\int_0^1 \hat{\pi}_1(a) da$ as in condition (i), or if as in the case of condition (ii), the rate of increase is not large but altruistic offsprings can be born from nonaltruistic parents to supplement the source of altruistic individuals in the population, altruism will still evolve in the community. Thus, when the difference in altruistic benefits for the altruists and non-altruists is not too lopsided, i.e. $\gamma_\beta(a) - \gamma_\alpha(a)$ is bounded above by $\hat{\pi}_1/2$ and below by $-\hat{\pi}_1$ on $[0, 1]$, the determining factor on whether altruism will evolve becomes the ability of the altruistic group to sustain its numbers through reproduction. In other words, the altruists must either be stronger physiologically (smaller mortality to allow larger bound on $\gamma_\beta(a) - \gamma_\alpha(a)$) or biologically more fertile in order to survive.

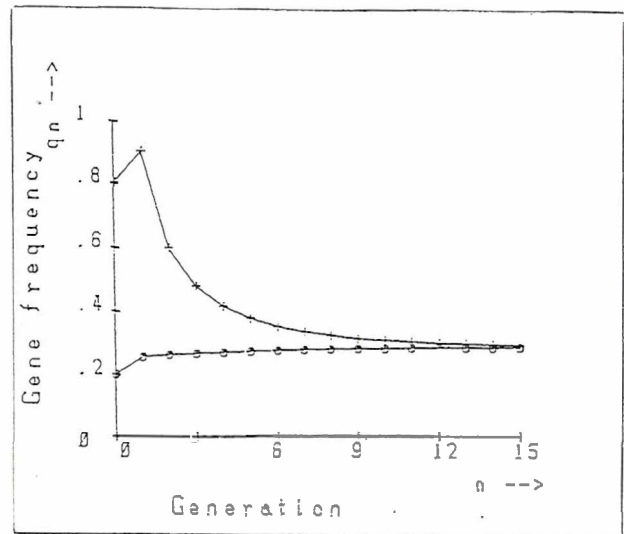


Fig. 1. Gene frequency $q_n(0)$ of A_2 of the n th generation at the time of birth plotted against n for a population with $\hat{\pi}_1(a) = a$, $\hat{\gamma}(a) = -a$ and $F(x) = x/(1+\sqrt{x})^2$. Initial gene frequency $q_0(0) = 0.2$ (o-o); $q_0(0) = 0.8$ (+-+).

Example and conclusions

In many models of population genetics, a gene could be recessive so that the gene frequency of the n th generation is given by the relation $q_n = q_{n-1}/(1+q_{n-1})$; see Wilson and Bossert (1971). If the altruistic allele A_2 is recessive and the fecundity relation after selection is given by

$$q_n^2(0) = F(q_{n-1}^2(1)) = q_{n-1}^2(1)/(1+q_{n-1}(1))^2, \tag{3.1}$$

we have $F'(0) = 1$, which is the same as in Hsieh (1988), and condition (i) is still satisfied. In Fig. 1, gene frequency versus generation time is plotted using equation (2.1), using data from Hsieh (1988). The result is a population converging to fixed altruism. Thus it is still possible for altruism to evolve even if there is directional selection against the altruists as long as condition (i) is met.

For Fig. 2, let

$$\gamma(a) = \begin{cases} 0 & 0 \leq a < 0.5 \\ -a & 0.5 \leq a \leq 1, \end{cases} \tag{3.2}$$

and all other data as in Fig. 1. Again, the population converges to pure altruism. This is the case where $\hat{\gamma}(a)$ satisfies the inequality in the Theorem, but is discontinuous. Thus, as mentioned earlier, the continuity condition is not necessary for the existence of a positive fixed point in the Theorem. The biological significance of this is that if the altruistic behavior is only performed by the adults of the species, then the functions γ_α

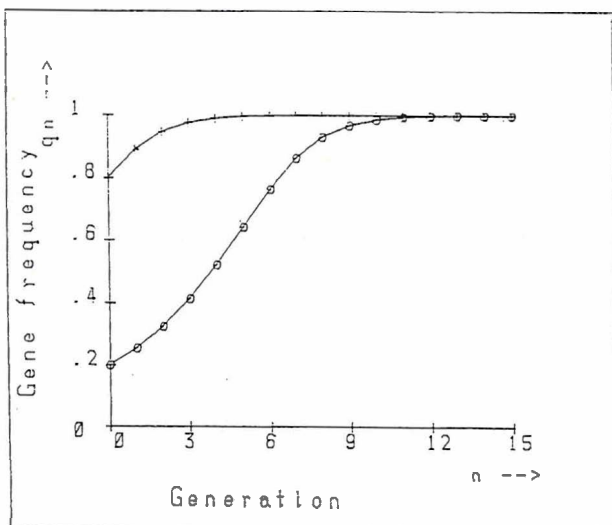


Fig. 2. Gene frequency $q_n(0)$ of A_2 of the n th generation at the time of birth plotted against n for a population with $\pi_1(a) = a$, $\gamma(a) = 0$, $0 \leq a < 0.5$; $-a$, $0.5 \leq a \leq 1$, and $f(x) = x$. Initial gene frequency $q_0(0) = 0.2$ (o—o); $q_0(0) = 0.8$ (+—+).

(a) and $\gamma_\beta(a)$ might be zero for the first stage of the individual's lifetime, but will be nonzero after a certain age, as the function in (3.2) is defined. In short, the age-dependent structure of this model enables us to consider cases in which the altruistic behavior is apparent only at certain stages of the individual's lifetime.

As a final remark, I would like to point out that although the model proposed in this article deals with the evolution of the altruistic trait in a single species, it could just as easily be used to discuss a multi-species community with one or more altruistic species. In fact, the results given for reproductive rate can be used to describe a community with one altruistic species and one selfish species if we assign distinct fecundity func-

tions for each species—a simplification of our work since we would not need the extra assumption on the fecundity function for gene frequency of the altruistic trait.

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