Gene–culture coevolution: Models for the evolution of altruism with cultural transmission

(pheno/genotypes/Hamilton's rule)

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ABSTRACT Models of sexual haploids under kin selection are constructed. The trait of altruism is transmitted vertically from parent to child, but not in a strictly genetic manner. Two systems of altruism are considered: parent-to-offspring and sib-to-sib. In the former case it is shown that even when Hamilton's conditions for the success of genetically determined altruism are met, genes that increase the transmission of altruism may not invade the population. With sib-to-sib altruism, such genes will always increase initially.

Hamilton (1) proposed a model for the evolution of altruism in which altruists increase the survival rate of their relatives while decreasing their own. In this model, altruism was under simple genetic control and this, together with the way in which the fitness effects were combined, led to a simple and intuitively plausible rule for the initial success of altruism. The way in which the fitness effects are combined is known to influence the conditions for evolution of altruism (2, 3). Departures from simple genetic transmission of altruism should also play a role in determining the conditions for its increase.

In this paper, we shall study the evolution of altruistic traits that are transmitted both by genetic means and by vertical (i.e., parent to child) cultural transmission. There is no general agreement as to the best way to construct such a model. Indeed, there has been considerable controversy in recent years concerning the appropriate theoretical methodology whereby the evolution of traits under both genetic and cultural control may be studied. Lumsden and Wilson (ref. 4; see also Wilson, ref. 5) have taken an approach which (they claim) leads to the production of major differences between populations as a result of small between-population genetic differences. Lumsden and Wilson also claim that their approach demonstrates that cultural transmission should accelerate the rate of genetic evolution. The arguments that lead to these conclusions have been questioned by Maynard Smith and Warren (6). Furthermore, Maynard Smith and Warren (6) show that assumptions that appear to be just as plausible as those used by Lumsden and Wilson lead to very different results.

Here we shall take a different approach and introduce a class of evolutionary genetic models that take into account both vertical cultural transmission of a trait and kin selection on the trait. Thus, our analysis is an attempt to generalize some of the evolutionary theory of altruism to the situation where the trait under kin selection is transmitted from parent to child, but not necessarily in a strictly genetic manner. We show (i) that nongenetic transmission entails significant departures from Hamilton's rules used in strictly genetic models to specify conditions on the fitness gain to receivers of altruism that allow the increase of the altruistic phenotype and (ii) that the conditions under which a gene that increases

the rate of cultural transmission of an altruistic trait can initially succeed are not as simple as in the genetic case, but that under special conditions, natural interpretations are available.

Transmission Model with Sexual Haploids

There are two genotypes, *A* and *a* and two phenotypes indicated by the subscripts 1 and 2. Thus, there are four pheno/genotypes, *A*₁, *A*₂, *a*₁, and *a*₂, whose frequencies are *u*₁, *u*₂, *u*₃, and *u*₄ in the parental generation at mating (7). Transmission of the phenotype is uniparental, and Table 1 gives the probabilities that a transmitting parent of the respective phenotype produces offspring of the respective pheno/genotypes. Mating is random and the mating and transmission are summarized in Table 2.

If *u*₁^T, *u*₂^T, *u*₃^T, *u*₄^T are the frequencies of the pheno/genotypes in the offspring after vertical (genetic and cultural) transmission, then

$$u_1^T = b_{A_1}W + b_{A_2}X \quad [1a]$$

$$u_2^T = (1 - b_{A_1})W + (1 - b_{A_2})X \quad [1b]$$

$$u_3^T = b_{a_1}Y + b_{a_2}Z \quad [1c]$$

$$u_4^T = (1 - b_{a_1})Y + (1 - b_{a_2})Z, \quad [1d]$$

where

$$W = u_1^2 + u_1u_2 + u_1u_3 + (u_1u_4 + u_2u_3)/2 \quad [2a]$$

$$X = u_1u_2 + u_2^2 + u_2u_4 + (u_1u_4 + u_2u_3)/2 \quad [2b]$$

$$Y = u_3^2 + u_3u_4 + u_1u_3 + (u_1u_4 + u_2u_3)/2 \quad [2c]$$

$$Z = u_4^2 + u_3u_4 + u_2u_4 + (u_1u_4 + u_2u_3)/2. \quad [2d]$$

Parent-to-Offspring Altruism: Model I

Models for parent-to-offspring altruism may be specified in a number of different ways. Here we shall use the additive combination of gain and loss in fitness specified by Cavalli-Sforza and Feldman (2) that is most commonly used in kin selection studies. Individuals of phenotype 1 suffer a fitness loss γ . Broods with a randomly chosen parent of phenotype 1 enjoy an average fitness increase proportional to β . One way to compute the resulting fitnesses uses the conditional kinship probabilities developed in ref. 2 to produce the ex-

Table 1. Pheno/genotypic transmission rates

Phenotype of transmitting parent	Probability of offspring pheno/genotype			
	<i>A</i> ₁	<i>A</i> ₂	<i>a</i> ₁	<i>a</i> ₂
1	<i>b</i> _{<i>A</i>1}	1 - <i>b</i> _{<i>A</i>1}	<i>b</i> _{<i>a</i>1}	1 - <i>b</i> _{<i>a</i>1}
2	<i>b</i> _{<i>A</i>2}	1 - <i>b</i> _{<i>A</i>2}	<i>b</i> _{<i>a</i>2}	1 - <i>b</i> _{<i>a</i>2}

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Table 2. Mating and transmission

Transmitting parent	Other parent*	Mating frequency	Probability of offspring pheno/genotype			
			A_1	A_2	a_1	a_2
A_1	A_1, A_2	$u_1(u_1 + u_2)$	b_{A_1}	$1 - b_{A_1}$	0	0
A_1	a_1, a_2	$u_1(u_3 + u_4)$	$b_{A_1}/2$	$(1 - b_{A_1})/2$	$b_{a_1}/2$	$(1 - b_{a_1})/2$
A_2	A_1, A_2	$u_2(u_1 + u_2)$	b_{A_2}	$1 - b_{A_2}$	0	0
A_2	a_1, a_2	$u_2(u_3 + u_4)$	$b_{A_2}/2$	$(1 - b_{A_2})/2$	$b_{a_2}/2$	$(1 - b_{a_2})/2$
a_1	A_1, A_2	$u_3(u_1 + u_2)$	$b_{A_1}/2$	$(1 - b_{A_1})/2$	$b_{a_1}/2$	$(1 - b_{a_1})/2$
a_1	a_1, a_2	$u_3(u_3 + u_4)$	0	0	b_{a_1}	$1 - b_{a_1}$
a_2	A_1, A_2	$u_4(u_1 + u_2)$	$b_{A_2}/2$	$(1 - b_{A_2})/2$	$b_{a_2}/2$	$(1 - b_{a_2})/2$
a_2	a_1, a_2	$u_4(u_3 + u_4)$	0	0	b_{a_2}	$1 - b_{a_2}$

*Offspring probabilities are the same for both phenotypes of this parent.

pressions in the square brackets below. The frequencies u'_1 , u'_2 , u'_3 , and u'_4 in offspring after transmission and selection are as follows.

$$\begin{aligned}
 u'_1 &\propto u_1^T \left[1 - \gamma + \beta \frac{P(\text{parent is phenotype 1 and child } A_1)}{P(\text{child is } A_1)} \right] \\
 u'_2 &\propto u_2^T \left[1 + \beta \frac{P(\text{parent is phenotype 1 and child } A_2)}{P(\text{child is } A_2)} \right] \\
 u'_3 &\propto u_3^T \left[1 - \gamma + \beta \frac{P(\text{parent is phenotype 1 and child } a_1)}{P(\text{child is } a_1)} \right] \\
 u'_4 &\propto u_4^T \left[1 + \beta \frac{P(\text{parent is phenotype 1 and child } a_2)}{P(\text{child is } a_2)} \right]
 \end{aligned} \quad [3]$$

In other words,

$$\begin{aligned}
 \bar{w}u'_1 &= u_1^T(1 - \gamma) \\
 &+ \beta \left[b_{A_1} \left(u_1^2 + u_1u_3 + \frac{u_1u_2}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right. \\
 &\left. + b_{A_2} \left(\frac{u_1u_2}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right], \quad [4a]
 \end{aligned}$$

$$\begin{aligned}
 \bar{w}u'_2 &= u_2^T \\
 &+ \beta \left[(1 - b_{A_1}) \left(u_1^2 + u_1u_3 + \frac{u_1u_2}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right. \\
 &\left. + (1 - b_{A_2}) \left(\frac{u_1u_2}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right], \quad [4b]
 \end{aligned}$$

$$\begin{aligned}
 \bar{w}u'_3 &= u_3^T(1 - \gamma) \\
 &+ \beta \left[b_{a_1} \left(u_3^2 + u_1u_3 + \frac{u_3u_4}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right. \\
 &\left. + b_{a_2} \left(\frac{u_3u_4}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right], \quad [4c]
 \end{aligned}$$

and

$$\begin{aligned}
 \bar{w}u'_4 &= u_4^T \\
 &+ \beta \left[(1 - b_{a_1}) \left(u_3^2 + u_1u_3 + \frac{u_3u_4}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right. \\
 &\left. + (1 - b_{a_2}) \left(\frac{u_3u_4}{2} + \frac{u_1u_4}{4} + \frac{u_2u_3}{4} \right) \right], \quad [4d]
 \end{aligned}$$

where $\bar{w}$ is the sum of the right sides of the equations.

Initial Increase of the Altruistic Phenotype

Consider the situation where phenotype 2 is fixed. What are the conditions that allow phenotype 1 to increase in frequency when it occurs first at low frequency near where phenotype 2 is fixed? The simplest situation would be where all A genotypes are A_1 and all a genotypes are a_2 ; i.e., where $b_{A_1} = b_{A_2} = 1$ and $b_{a_1} = b_{a_2} = 0$. This situation is identical to that of strict genetic transmission of altruism. Here there is initial fixation of a_2 (i.e., $u_4 = 1$) which is unstable to the introduction of A_1 when $\beta/2 > \gamma$, the usual Hamilton condition (1, 2). More generally, for phenotype 2 to be fixed with A and a coexisting, it is required that $b_{A_2} = b_{a_2} = 0$. Then there is a line of neutral equilibrium points $\hat{u}_2, \hat{u}_4$, with $\hat{u}_2 + \hat{u}_4 = 1$. From any such point, the local increase of A_1 and a_1 is described by the linear system in u_1 and u_3 :

$$\begin{aligned}
 u'_1 &= b_{A_1} \left(1 - \gamma + \frac{\beta}{2} \right) \left(\hat{u}_2 + \frac{\hat{u}_4}{2} \right) u_1 \\
 &+ \frac{b_{A_1}}{2} \hat{u}_2 \left(1 - \gamma + \frac{\beta}{2} \right) u_3; \quad [5a]
 \end{aligned}$$

$$\begin{aligned}
 u'_3 &= \frac{b_{a_1}}{2} \left(1 - \gamma + \frac{\beta}{2} \right) \hat{u}_4 u_1 \\
 &+ b_{a_1} \left(1 - \gamma + \frac{\beta}{2} \right) \left(\frac{\hat{u}_2}{2} + \hat{u}_4 \right) u_3. \quad [5b]
 \end{aligned}$$

The characteristic polynomial of Eqs. 5 is

$$\begin{aligned}
 \lambda^2 - \lambda \left(1 - \gamma + \frac{\beta}{2} \right) \left[b_{A_1} \left(\hat{u}_2 + \frac{\hat{u}_4}{2} \right) + b_{a_1} \left(\hat{u}_4 + \frac{\hat{u}_2}{2} \right) \right] \\
 + \frac{b_{A_1}b_{a_1}}{2} \left(1 - \gamma + \frac{\beta}{2} \right)^2. \quad [6]
 \end{aligned}$$

The condition for the initial increase of phenotype 1 is that the larger root of Eq. 6 be greater than unity in absolute value. If we set $G = b_{A_1}(1 + \hat{u}_2) + b_{a_1}(1 + \hat{u}_4)$, this condition is

$$\frac{\beta}{2} > \gamma - 1 + \frac{G - (G^2 - 8b_{A_1}b_{a_1})^{1/2}}{2b_{A_1}b_{a_1}}. \quad [7]$$

When $b_{A_1} = b_{a_1} = b$, for instance, Eq. 6 reduces to the simple form

$$\frac{\beta}{2} > \gamma + (b^{-1} - 1). \quad [8]$$

Since $b \leq 1$, condition 8 illustrates that there is a *transmission load* which makes the increase of altruism more difficult

as its transmission deteriorates—i.e., b decreases. With perfect transmission ($b = 1$) condition 8 takes the form expected by simple application of Hamilton's rule. In general, inequality 7 reveals that it is more difficult for altruism to increase under the present form of cultural transmission than under simple genetic assumptions. This agrees with conclusions drawn earlier (6, 8).

Parent-to-Offspring Altruism: Model II

In Model I, the choice of the parent to interact with the offspring is made at random from the parental pair. In Model II, the offspring gains only when the transmitting parent is altruistic. In this case Eqs. 4 are altered to become

$$\bar{w}u'_1 = u_1^T(1 - \gamma) + \beta b_{A_1} \left(u_1^2 + u_1u_2 + u_1u_3 + \frac{u_1u_4}{2} + \frac{u_2u_3}{2} \right), \quad [9a]$$

$$\bar{w}u'_2 = u_2^T + \beta(1 - b_{A_1}) \times \left(u_1^2 + u_1u_2 + u_1u_3 + \frac{u_1u_4}{2} + \frac{u_2u_3}{2} \right), \quad [9b]$$

$$\bar{w}u'_3 = u_3^T(1 - \gamma) + \beta b_{A_1} \left(u_3^2 + u_1u_3 + u_3u_4 + \frac{u_1u_4}{2} + \frac{u_2u_3}{2} \right), \quad [9c]$$

and

$$\bar{w}u'_4 = u_4^T + \beta(1 - b_{A_2}) \times \left(u_3^2 + u_1u_3 + u_3u_4 + \frac{u_1u_4}{2} + \frac{u_2u_3}{2} \right), \quad [9d]$$

where $\bar{w} = 1 - \gamma(u_1^T + u_3^T) + \beta(W + Y)$ (see Eq. 2). In this case $\beta/2$ is replaced everywhere in Eqs. 5 by β and condition 8 becomes $\beta > \gamma + (b^{-1} - 1)$, which, of course, does not reduce to the Hamilton condition for $b = 1$.

Initial Increase of a New Allele That Affects Transmission

Here we suppose that a_1 and a_2 are initially in equilibrium (under cultural transmission as in ref. 9). We seek the conditions under which the allele A will increase in frequency when introduced near the a_1, a_2 equilibrium. This equilibrium is given by $\hat{u}_3$ and $\hat{u}_4 = 1 - \hat{u}_3$, where $\hat{u}_3$ is the unique admissible root of the quadratic equation

$$u_3^2[(\beta/2 + \gamma)(b_{A_2} - b_{A_1}) - \beta] + u_3[\beta(b_{A_2} + b_{A_1})/2 + (1 - \gamma)(b_{A_2} - b_{A_1}) - 1 + \gamma b_{A_2}] + b_{A_2}(1 - \gamma) = 0. \quad [10]$$

Convergence to the root of Eq. 10 has not been proven in general. It should be noted that under transmission alone, in the absence of selection, stable cycles may occur (10), although under viability selection they do not. In the present kin selection case, some 200 randomly chosen sets of b_{A_2} , b_{A_1} , β , and γ did not produce a single case of cycling or other anomalous behavior upon numerical iteration. We have succeeded in analyzing the initial increase problem under the special condition $b_{A_1} = b_{A_2} = b$, say, and $b_{A_1} = b_{A_2} = b^*$. Then Eq. 10 reduces to

$$\beta u_3^2 + u_3(1 - \gamma b - \beta b) - b(1 - \gamma) = 0, \quad [11]$$

and the local stability of the root of Eq. 11 to the introduction of allele A is governed by the roots of the characteristic polynomial $Q(\lambda)$:

$$Q(\lambda) = (\lambda \bar{w})^2 - \lambda \bar{w} \left(1 - \gamma b^* + \frac{\beta b^*}{2} + \frac{\beta \hat{u}_3}{2} \right) + \frac{\beta \gamma b^*(1 - b^*)}{2}. \quad [12]$$

A will increase when rare if the larger root of $Q(\lambda)$ is greater than unity. This occurs if

$$Q(1) = (b^* - b) \left[(\hat{u}_3 \beta + 1) \left(\gamma - \frac{\beta}{2} \right) + \frac{\beta \gamma (1 - b^*)}{2} - \gamma^2 b \right] < 0. \quad [13]$$

A cursory examination of condition 13 suggests that a simple relationship between $(\gamma - \beta/2)$, the Hamilton expression, and $(b^* - b)$, the transmission difference, is not likely to validate the inequality. The following four numerical examples indicate the complications that arise here.

Example 1: $\beta = 1.0$, $\gamma = 0.6$, $b = 0.8$, $b^* = 0.9$. Here $\beta/2 < \gamma$ and $b^* > b$, yet A increases when rare.

Example 2: $\beta = 1.0$, $\gamma = 0.4$, $b = 0.8$, $b^* = 0.9$. Here $\beta/2 > \gamma$ and $b^* > b$, and A increases when rare.

Example 3: $\beta = 0.3$, $\gamma = 0.2$, $b = 0.2$, $b^* = 0.1$. Here $\beta/2 < \gamma$ and $b > b^*$, yet A increases when rare.

Example 4: $\beta = 1.1$, $\gamma = 0.5$, $b = 0.1$, $b^* = 0.2$. Here $\beta/2 > \gamma$ and $b^* > b$, yet A does not increase when rare.

Remark. In the special case $b_{A_1} = b_{A_2} = b$, with $b_{A_1} = b_{A_2} = b^*$, Model I and Model II produce the same characteristic polynomial 12. In more general cases, there will be differences between the models, which are not pursued here.

Clearly the nongenetic transmission of the "altruistic" phenotypes interferes with the validity of any straightforward application of Hamilton's rules. Nevertheless, there are two other ways to express condition 13 that are informative. Write $\bar{w}_a = 1 - \gamma b + \beta \hat{u}_3$, the average fitness of a_1 and a_2 prior to the introduction of A . Then condition 13 is

$$(b^* - b) \left[\hat{w} \left(\gamma - \frac{\beta}{2} \right) + \frac{(1 - b - b^*)\beta\gamma}{2} \right] < 0. \quad [14a]$$

Thus, only if $b + b^* = 1$, a very special case, does this produce a condition where Hamilton's rules apply.

Alternatively, if we denote by $\hat{x}_{A_1}$ the limiting fraction of phenotype 1 among allele A as the equilibrium $(\hat{u}_3, \hat{u}_4)$ is approached, condition 13 reduces to

$$\frac{\beta}{2} (\hat{x}_{A_1} - \hat{u}_3) > \gamma(b^* - b). \quad [14b]$$

Sib-to-Sib Altruism

Here the fitness gain accrues to individuals with a sib of phenotype 1. In this case the conditional kinship approach produces the following recursions after transmission and selection:

$$u'_1 \propto u_1^T \left[1 - \gamma + \beta \frac{P(\text{offspring is } A_1 \text{ and sib is phenotype 1})}{P(\text{offspring is } A_1)} \right];$$

$$\begin{aligned}
 u'_2 &\propto u_2^T \left[1 + \beta \frac{P(\text{offspring is } A_2 \text{ and sib is phenotype 1})}{P(\text{offspring is } A_2)} \right]; \\
 u'_3 &\propto u_3^T \left[1 - \gamma + \beta \frac{P(\text{offspring is } a_1 \text{ and sib is phenotype 1})}{P(\text{offspring is } a_1)} \right]; \\
 u'_4 &\propto u_4^T \left[1 + \beta \frac{P(\text{offspring is } a_2 \text{ and sib is phenotype 1})}{P(\text{offspring is } a_2)} \right].
 \end{aligned}$$

In other words,

$$\begin{aligned}
 \bar{w}u'_1 &= u_1^T(1 - \gamma) + \beta\{b_{A_1}(u_1 + u_2)[b_{A_1}u_1 + (b_{A_1} + b_{a_1})u_3/4] \\
 &\quad + b_{A_2}(u_1 + u_2)[b_{A_2}u_2 + (b_{A_2} + b_{a_2})u_4/4] \\
 &\quad + (u_3 + u_4)[b_{A_1}(b_{A_1} + b_{a_1})u_1 \\
 &\quad + b_{A_2}(b_{A_2} + b_{a_2})u_2]/4\}, \quad [15a]
 \end{aligned}$$

$$\begin{aligned}
 \bar{w}u'_2 &= u_2^T + \beta\{(1 - b_{A_1})(u_1 + u_2)[b_{A_1}u_1 + (b_{A_1} + b_{a_1})u_3/4] \\
 &\quad + (1 - b_{A_2})(u_1 + u_2)[b_{A_2}u_2 + (b_{A_2} + b_{a_2})u_4/4] \\
 &\quad + (u_3 + u_4)[(1 - b_{A_1})(b_{A_1} + b_{a_1})u_1 \\
 &\quad + (1 - b_{A_2})(b_{A_2} + b_{a_2})u_2]/4\}, \quad [15b]
 \end{aligned}$$

$$\begin{aligned}
 \bar{w}u'_3 &= u_3^T(1 - \gamma) + \beta\{b_{a_1}(u_3 + u_4)[b_{a_1}u_3 + (b_{A_1} + b_{a_1})u_1/4] \\
 &\quad + b_{a_2}(u_3 + u_4)[b_{a_2}u_4 + (b_{A_2} + b_{a_2})u_2/4] \\
 &\quad + (u_1 + u_2)[b_{a_1}(b_{A_1} + b_{a_1})u_3 \\
 &\quad + b_{a_2}(b_{A_2} + b_{a_2})u_4]/4\}, \quad [15c]
 \end{aligned}$$

and

$$\begin{aligned}
 \bar{w}u'_4 &= u_4^T + \beta\{(1 - b_{a_1})(u_3 + u_4)[b_{a_1}u_3 + (b_{A_1} + b_{a_1})u_1/4] \\
 &\quad + (1 - b_{a_2})(u_3 + u_4)[b_{a_2}u_4 + (b_{A_2} + b_{a_2})u_2/4] \\
 &\quad + (u_1 + u_2)[(1 - b_{a_1})(b_{A_1} + b_{a_1})u_3 \\
 &\quad + (1 - b_{a_2})(b_{A_2} + b_{a_2})u_4]/4\}, \quad [15d]
 \end{aligned}$$

where $\bar{w}$ is the sum of the right-hand sides.

Initial Increase of the Altruistic Phenotype

As in the case of parent-to-offspring altruism, if $b_{A_1} = 1$, $b_{a_1} = 0$, $b_{A_2} = 1$, and $b_{a_2} = 0$ (the strictly genetic situation), then the condition for initial increase of A_1 from fixation of a_2 is $\beta/2 > \gamma$. More generally, if $b_{A_2} = b_{a_2} = 0$ and initially the population is fixed for phenotype 2 with A and a segregating at frequencies $\hat{u}_2$ and $\hat{u}_4$, respectively, the initial increase of phenotype 1 is governed by the eigenvalues of matrix $T = ||t_{ij}||$ with

$$\begin{aligned}
 t_{11} &= b_{A_1} \left[(1 - \gamma) \left(\hat{u}_2 + \frac{\hat{u}_4}{2} \right) + \beta \left(b_{A_1} \hat{u}_2 + \frac{b_{A_1} + b_{a_1}}{4} \hat{u}_4 \right) \right], \\
 t_{12} &= b_{A_1} \left[(1 - \gamma) \frac{\hat{u}_2}{2} + \beta \frac{(b_{A_1} + b_{a_1})}{4} \hat{u}_2 \right],
 \end{aligned}$$

$$t_{21} = b_{a_1} \left[(1 - \gamma) \frac{\hat{u}_4}{2} + \beta \frac{(b_{A_1} + b_{a_1})}{4} \hat{u}_4 \right],$$

and

$$t_{22} = b_{a_1} \left[(1 - \gamma) \left(\frac{\hat{u}_2}{2} + \hat{u}_4 \right) + \beta \left(b_{a_1} \hat{u}_4 + \frac{(b_{A_1} + b_{a_1})}{4} \hat{u}_2 \right) \right].$$

When $b_{A_1} = b_{a_1} = 1$, the eigenvalues of T are $1 - \gamma + \beta$ and $(1 - \gamma + \beta)/2$. Hence, the condition for initial increase of A_1 , a_1 is $\beta > \gamma$. When $b_{A_1} = b_{a_1} = b$, the eigenvalues are $b(1 - \gamma + \beta b)$ and $b(1 - \gamma + \beta b)/2$. The condition for initial increase is then

$$\beta b > \gamma + (b^{-1} - 1). \quad [16]$$

This condition differs from that in the parent-to-offspring case. It is especially interesting that when $b = 1$, the initial-increase condition does not reduce to Hamilton's rule. Note, however, that when $b_1 = b_2 = 1$, condition 16 is identical to the parent-offspring result when only the parent transmitting phenotype 1 (altruism) is the fitness donor (that is, Model II).

Initial Increase of a New Allele

Take a_1 and a_2 in equilibrium to start. Initially, therefore, $u_1 = u_2 = 0$ so that in Eqs. 1 and 2 $W = X = 0$. Thus, as before, $u_3^T = b_{a_1}u_3 + b_{a_2}u_4$ and $u_4^T = (1 - b_{a_1})u_3 + (1 - b_{a_2})u_4$. As in the analysis of the parent-to-offspring case, we may simplify matters by taking $b_{A_1} = b_{A_2} = b^*$ and $b_{a_1} = b_{a_2} = b$. Thus, b is the transmission rate associated with the resident a gene and b^* that associated with the rare A gene. In this case, the equilibrium of a_1 and a_2 to begin the process is specified by $\hat{u}_3 = b/[1 + \beta b - \gamma]/[1 + (\beta - \gamma)b]$. The local analysis of the u_1, u_2 transformation near this equilibrium produces the conclusion that A increases when rare if

$$\left(\frac{\beta}{2} - \gamma \right) (b^* - b) > 0. \quad [17]$$

Now $\beta/2 > \gamma$ is the condition derived by Hamilton for the initial increase of an altruistic allele under purely genetic transmission. We see that if this condition holds, then a new gene A that imparts greater uniparental transmission of the kin-selected trait (i.e. $b^* > b$) will succeed. Thus, in addition to Hamilton's condition it must also be true in this case that altruism be more easily learned by individuals carrying A than by individuals carrying a .

Conclusions

There are obviously several ways to construct population models for the learning of altruism. We have considered only vertical uniparental transmission and additive combination of fitness loss and gain. The effects of departures from these assumptions are under investigation, but they seem a natural place to start, and from our results it is clear that nongenetic transmission of the altruistic phenotype causes departures from Hamilton's rule. These departures appear to be most pronounced when the transmitter of the altruism and the altruist are the same, as in the parent-to-offspring case. It is also seen that whether altruism is performed by a randomly chosen parent or by just the transmitting parent may also be important. The effects of other types of cultural transmission (9) remain to be considered.

We have taken care to differentiate two classes of problems. The first involves the increase of a rare altruistic phenotype starting from a situation in which alleles with differ-

ent learning capacities are both present. The second examines the increase, when rare, of an allele that affects the teaching or learning of altruism. The former of these problems is the usual one addressed in kin-selection theory, but strictly in terms of increase of an allele from a genetically (and phenotypically) monomorphic state. As to the second problem, when only four transmission coefficients (reduced to two in most of the analysis) are used, it is not possible to separate teaching and learning abilities. It should be stressed that the case $b_{A_1} = b_{A_2}$, $b_{a_1} = b_{a_2}$ analyzed in detail here is special and that the four-parameter transmission problem is unlikely to yield such elegant solutions.

A final remark that may suggest a connection between the above results and those in the standard kin-selection literature is in order. Uyenoyama and Feldman (11) and Uyenoyama *et al.* (12) suggested that initial increase of the rare allele should occur if $\beta b_{D \rightarrow R} > \gamma$, where $b_{D \rightarrow R}$ is the regression of the recipient's additive genetic value on that of the donor of the altruism. The regression must be computed in the limit as the original equilibrium is approached. In the parent-to-offspring case, a regression is obtained by considering the parent as the recipient and the offspring as the donor. Offspring are phenotype 1 and value b^* with probability ($u_1 + u_2$) and phenotype 1 of value b with probability ($u_3 + u_4$). Phenotype 2 has value 0. Only transmitting parents are counted and given value 1 if of phenotype 1 and 0 if of phenotype 2. The limiting value, as ($\hat{u}_3, \hat{u}_4$) is approached, of the regression of parent on offspring in this sense is $(\hat{x}_{A_1} - \hat{u}_3)/2(b^* - b)$, which is the quantity relevant to the initial increase condition 14b. We have not devised a natural regression in which these donor/recipient roles are reversed.

In the sib case, a regression of recipient sib on donor sib may be computed. The values for the sibs are b^* for A_1 , b for a_1 and 0 for A_2 and a_2 . A straightforward calculation reveals that the sib-to-sib regression is $1/2$, the usual value for the initial increase condition under sib-to-sib kin selection.

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