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General kin selection models for genetic evolution of sib altruism in diploid and haplodiploid species

(haplodiploidy/population genetics/stability analysis/Hymenoptera/convexity)

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ABSTRACT A population genetic approach is presented for general analysis and comparison of kin selection models of sib and half-sib altruism. Nine models are described, each assuming a particular mode of inheritance, number of female inseminations, and Mendelian dominance of the altruist gene. In each model, the selective effects of altruism are described in terms of two general fitness functions, A(β) and S(β), giving respectively the expected fitness of an altruist and a nonaltruist as a function of the fraction of altruists β in a given sibship. For each model, exact conditions are reported for stability at altruist and nonaltruist fixation. Under the Table 3 axions, the stability conditions may then be partially ordered on the basis of implications holding between pairs of conditions. The partial orderings are compared with predictions of the kin selection theory of Hamilton.

Kin selection, i.e., selection for altruistic behavior between genetic relatives, has become the major genetic explanation of many evolutionary phenomena involving social behavior (1–3). Recognition of the fundamental importance of kin selection largely began with the work of Hamilton (4, 5), who pointed out that haplodiploidy in the Hymenoptera may have been a major factor facilitating at least eleven independent emergences of eusociality in this order (ref. 3, p. 327). Specifically, Hamilton noticed that haplodiploidy implies a mean Wright coefficient of sister-sister relationship $r = \frac{3}{4}$, which exceeds the mean relationship between a female parent and her offspring of either sex ($r = \frac{1}{2}$). He then made an attractive, if heuristic, argument that a kin altruist gene will be favorably selected if

$$k \equiv \frac{\text{mean fitness gained by recipient}}{\text{mean fitness lost by donor}} > \frac{1}{r}, \quad [1]$$

where r is the mean coefficient of relationship between donor and recipient (6). Using [1], Hamilton concluded that sociality in the Hymenoptera may be explained as a likely consequence of kin selection, specifically of sib selection (i.e., selection for altruism between sibs).

Although Hamilton's reasoning is not rigorous, it has directly served as the basis of a rapidly increasing body of subsequent work on kin selection (e.g., refs. 7–9). Many of these investigations have focused specifically on sib selection, and sib selection is undoubtedly one of the two or three cases of kin selection most frequently encountered in nature. Below, the problem of sib selection is reexamined rigorously as a mathematical problem in population genetics.

The present models start by assuming a single biallelic locus (A,a) which is undergoing sib selection, where a is taken to be the altruist trait. The first step is to write down a family of very general models describing sib selection under a variety of different modes of inheritance, number of female inseminations, and assumptions on Mendelian dominance. Assuming random mating in a large population, these models are then analyzed with respect to stability at both altruist and nonaltruist fixation. Next, these stability conditions are systematically examined for implications holding between pairs of conditions. This comparison is analogous to Hamilton's predictions using [**1**]. Specifically, a set of axioms is presented (Table 3) under which comparison of the altruist stability conditions leads to a nearly linear implication ordering (Fig. 1). This ordering largely agrees with Hamilton's predictions, as also to a lesser extent does the corresponding implication ordering for the nonaltruist conditions (Fig. 2). At the same time, the present analysis shows many ways in which the actual relations among different model cases are substantially more complicated than [1] would imply. In addition, the analysis makes clear that the presence of a Hamilton-type ordering of cases (and with it the validity of his predictions) is closely tied to the presence of certain key restrictions on the way altruism affects fitness [e.g., the presence of downward convexity in S(β)].

Description of models

For illustrative purposes, we first develop the case where a is recessive, inheritance is diploid, and each female is inseminated exactly once. There are then three genotypes (AA, Aa, aa), of which aa will be phenotypically altruist and AA and Aa will be phenotypically nonaltruist.

The first problem is one of assigning fitnesses within a sibship possessing a given altruist/nonaltruist composition. One is initially tempted to try to give a detailed model of the mechanics of altruism within the sibship, and to infer expected fitness on the basis of such a model. Essentially this approach has in fact been followed by a number of investigators (10, 11). However, it is always possible to suggest many variants on any particular description of the details of altruism, and it is correspondingly difficult to assess the robustness of conclusions drawn from such specific models. For this reason, the present developments will be carried out in a way which does not attempt to construct a detailed picture of altruism within a sibship. Instead, we simply start by defining two functions, S(β) and A(β):

S(β) = expected fitness of a nonaltruist in a sibship containing a proportion β of phenotypic altruists;
A(β) = expected fitness of an altruist, β as before.

For the initial purpose of writing down the desired diploid model and obtaining its associated fixation stability conditions, no restrictions will be placed on S(β) and A(β) other than S(β), A(β) ≥ 0. Later, when undertaking model comparisons, we will consider the effects of imposing restrictions on the form of S(β) and A(β) (Table 3).

Given S(β) and A(β), Table 1(a) reproduces a fitness tableau for the present model. Interpreting S(β) and A(β) as survival probabilities, the entries in the tableau are just the expected number of sibs of a given genotype surviving to reproduce, cross-classified by parental mating type (i.e., the combination of parental genotypes). The assumption is being made that all sibships are of the same size N and that N is large, so that one can work solely in terms of genotype frequency expectations. Large zygotic sibship size is in fact a plausible assumption for the social insects and numerous other species where sib selection may have taken place. Nevertheless, the assumption of large N is a limitation on the present models (the same assumption is also implicit in the models of both refs. 10 and 11).

To achieve a complete model, the final assumption is that there is random mating in a large population. Then let the frequencies of the genotypes (*AA, Aa, aa*) in the nth generation be (P_n, $2Q_n$, R_n). Let the 6 × 3 matrix of Table 1(a) be designated M_1, and let

$$f = (P_n^2, 4P_nQ_n, 2P_nR_n, 4Q_n^2, 4Q_nR_n, R_n^2) \qquad [2]$$

be the vector of random mating frequencies of the six parental genotype combinations in the column order of Table 1(a). Then one obtains the following recursion describing sib selection in the present model:

$$(P_{n+1}, 2Q_{n+1}, R_{n+1}) = \frac{fM_1}{\Sigma_n} \qquad [3]$$

$$\Sigma_n = \text{constant to make } P_{n+1} + 2Q_{n+1} + R_{n+1} = 1.$$

Note that [3] is a two-dimensional recursion in genotype frequencies (P_n, $2Q_n$, R_n), not a one-dimensional recursion in the *a* gene frequency $\eta_{n+1} = \phi(\eta_n)$. This necessity of proceeding in terms of genotype frequencies in giving an exact description of sib selection, with the attendant analytical complications, is a consequence of the fact that one must keep track of the frequency of different parental mating combinations in assigning fitness. Note also that N (sibship size) does not enter into [3].

In addition to the present case, additional model cases will also be considered:

1. Diploid inheritance, *a* recessive, single insemination;
2. Diploid, *a* dominant, single insemination;
3. Diploid, *a* recessive, multiple insemination;
4. Diploid, *a* dominant, multiple insemination;
5. Haplodiploid, brother altruist trait;
6. Haplodiploid, recessive sister altruist trait *a*, single insemination;
7. Haplodiploid, dominant sister altruist trait *a*, single insemination;
8. Haplodiploid, recessive sister altruist trait *a*, multiple insemination;
9. Haplodiploid, dominant sister altruist trait *a*, multiple insemination.

Case 2 is parallel to Case 1 with only the Mendelian dominance changed.

Table 1. Fitness tableaus for sib selection models (Cases 1, 3, 5, and 6)

(a) Case 1: Diploid, *a* recessive, single insemination

	(*AA*)	(*Aa*)	(*aa*)
(*AA* × *AA*)	NS(0)	0	0
(*AA* × *Aa*)	$\frac{N}{2}S(0)$	$\frac{N}{2}S(0)$	0
(*AA* × *aa*)	0	NS(0)	0
(*Aa* × *Aa*)	$\frac{N}{4}S(1/4)$	$\frac{N}{2}S(1/4)$	$\frac{N}{4}A(1/4)$
(*Aa* × *aa*)	0	$\frac{N}{2}S(1/2)$	$\frac{N}{2}A(1/2)$
(*aa* × *aa*)	0	0	NA(1)

(b) Case 3: Diploid, *a* recessive, multiple insemination

	(*AA*)	(*Aa*)	(*aa*)
(*AA*)	$\xi_n S(0)$	$\eta_n S(0)$	0
(*Aa*)	$\frac{\xi_n}{2} S\left(\frac{\eta_n}{2}\right)$	$\frac{1}{2} S\left(\frac{\eta_n}{2}\right)$	$\frac{\eta_n}{2} A\left(\frac{\eta_n}{2}\right)$
(*aa*)	0	$\xi_n S(\eta_n)$	$\eta_n A(\eta_n)$

(c) Case 5: Haplodiploid brother altruism

	(*AA*)	(*Aa*)	(*aa*)	(*A*)	(*a*)
(*AA* × *A*)	F	0	0	MS(0)	0
(*AA* × *a*)	0	F	0	MS(0)	0
(*Aa* × *A*)	$\frac{F}{2}$	$\frac{F}{2}$	0	$\frac{MS(1/2)}{2}$	$\frac{MA(1/2)}{2}$
(*Aa* × *a*)	0	$\frac{F}{2}$	$\frac{F}{2}$	$\frac{MS(1/2)}{2}$	$\frac{MA(1/2)}{2}$
(*aa* × *A*)	0	F	0	0	MA(1)
(*aa* × *a*)	0	0	F	0	MA(1)

(d) Case 6: Haplodiploid sister altruism, *a* recessive, single insemination

	(*AA*)	(*Aa*)	(*aa*)	(*A*)	(*a*)
(*AA* × *A*)	FS(0)	0	0	M	0
(*AA* × *a*)	0	FS(0)	0	M	0
(*Aa* × *A*)	$\frac{F}{2}S(0)$	$\frac{F}{2}S(0)$	0	$\frac{M}{2}$	$\frac{M}{2}$
(*Aa* × *a*)	0	$\frac{F}{2}S(1/2)$	$\frac{F}{2}A(1/2)$	$\frac{M}{2}$	$\frac{M}{2}$
(*aa* × *A*)	0	FS(0)	0	0	M
(*aa* × *a*)	0	0	FA(1)	0	M

Interpreting S(β), A(β) as probabilities of surviving to reproduce, the entries in the tables may be interpreted as simply the expected number of survivors of each genotype, cross-classified by the parental genotype combination. N = brood size (diploid case), F = female brood size, M = male brood size (haplodiploid cases).

In Cases 3 and 4 (and also Cases 8 and 9), "multiple insemination" refers to the assumption that altruism is now taking place within the set of offspring of a given female who has been inseminated by a large number of males, drawn at random from the male population at large. Strictly speaking, these cases are instances of half-sib, not sib, altruism, since in general the offspring of a given female will be related only through the mother. Table 1(b) is the fitness tableau for Case 3. Noting that genotype frequencies will still be the same in the two sexes, since there is no differential selection acting on males, one may unambiguously use (P_n, $2Q_n$, R_n) as before to denote the frequency of genotypes in the nth generation. One obtains a recursion

$$(P_{n+1}, 2Q_{n+1}, R_{n+1}) = \frac{(P_n, 2Q_n; R_n)M_3}{\Sigma_n}, \qquad [4]$$

where M_3 is the 3 × 3 matrix in Table 1(b) ($\xi_n = P_n + Q_n = 1 - \eta_n$) and Σ_n is a normalization constant to make $P_{n+1} + 2Q_{n+1} + R_{n+1} = 1$.

The importance of considering multiple insemination derives from Hamilton's observation (4) that altruism taking place among female haplodiploid half-sibs will correspond to a mean relationship coefficient $r = 1/4$, which is *lower* than the mean relatedness between a female parent and her offspring ($r = 1/2$). Hence for Hamilton's theory on the origins of Hymenopteran sociality to be credible, one must add the provision that multiple insemination should not be a prevailing species practice.

Table 2. Fixation stability conditions for sib and half-sib (multiple insemination) models, general $A(\beta)$-$S(\beta)$ form

Description	Altruist	Nonaltruist
1. Diploid, altruist trait recessive, single insemination (dip)	$S(\tfrac{1}{2}) < A(1)*$	$S(\tfrac{1}{4}) + A(\tfrac{1}{4}) < 2S(0)$
2. Diploid, altruist trait dominant, single insemination (dip-dom)	$S(\tfrac{3}{4}) + A(\tfrac{3}{4}) < 2A(1)$	$A(\tfrac{1}{2}) < S(0)*$
3. Diploid, altruist trait recessive, multiple insemination (dip-mi)	$S(1) + S(\tfrac{1}{2}) < 2A(1)*$	$2A(0) + \tfrac{1}{2} S'(0) < 2S(0)$
4. Diploid, altruist trait dominant, multiple insemination (dip-dom-mi)	$2S(1) - \frac{A'(1)}{2} < 2A(1)$	$A(0) + A(\tfrac{1}{2}) < 2S(0)*$
5. Haplodiploid, brother-brother† altruism (BB)	$S(\tfrac{1}{2}) < A(1)*$	$A(\tfrac{1}{2}) < S(0)*$
6. Haplodiploid, recessive sister altruist trait, single insemination (SS)	$S(\tfrac{1}{2}) + S(0) < 2A(1)*$	$S(\tfrac{1}{2}) + 2A(\tfrac{1}{2}) < 3S(0)$
7. Haplodiploid, dominant sister altruist trait, single insemination (SS-dom)	$A(\tfrac{1}{2}) + 2S(\tfrac{1}{2}) < 3A(1)$	$A(\tfrac{1}{2}) + A(1) < 2S(0)*$
8. Haplodiploid, recessive sister altruist trait, multiple insemination (SS-mi)	$S(1) + S(\tfrac{1}{2}) < 2A(1)*$	$2A(0) + \tfrac{1}{2} S'(0) < 2S(0)$
9. Haplodiploid, dominant sister altruist trait, multiple insemination (SS-dom-mi)	$2S(1) - \frac{A'(1)}{2} < 2A(1)$	$A(0) + A(\tfrac{1}{2}) < 2S(0)*$
10. Diploid, single insemination, heterozygote penetrance with probability $h \in (0, 1)$	$(1 - h)S\left(\frac{1+h}{2}\right) + hA\left(\frac{1+h}{2}\right) < A(1)*$	$(1 - h)S\left(\frac{h}{2}\right) + hA\left(\frac{h}{2}\right) < S(0)*$

Abbreviations used in figures are given in parentheses.

* Indicated condition may be obtained by a linear stability analysis about the relevant fixation.

† Here classification by dominance and insemination is irrelevant.

Table 1(c)–(d) describe, respectively, Cases 5 and 6. In all haplodiploid cases, it is assumed that the altruist gene affects behavior in one sex, and this sex is designated in the model description (Cases 5–9 above). The *a* gene is then taken to be selectively neutral in the unaffected sex. Note that there is only one haplodiploid brother altruism case, since male haploidy and parthenogenesis make irrelevant any distinctions based on Mendelian dominance or the number of female inseminations.

In setting up recursions for the haplodiploid cases, it is in general necessary to keep separate track of male and female genotype frequencies, since selection is now acting differentially on the two sexes. We sketch how the recursion is set up in Case 6. First note that because there is no selection on the males, the male (*A*,*a*) gene frequencies will be (ξ_{n-1}, η_{n-1}), where $\xi_{n-1} = P_{n-1} + Q_{n-1}$, $\eta_{n-1} = Q_{n-1} + R_{n-1}$. Let M_6 be the 6×3 matrix given by the first three columns of the 6×5 matrix in Table 1(d). Let

$$h = (P_n\xi_{n-1}, P_n\eta_{n-1}, 2Q_n\xi_{n-1}, 2Q_n\eta_{n-1}, R_n\xi_{n-1}, R_n\eta_{n-1}), \quad [5]$$

which is just the random mating frequency vector analogous to f in [2]. One then obtains a recursion in the female genotype frequencies $(P_n, 2Q_n, R_n)$,

$$(P_{n+1}, 2Q_{n+1}, R_{n+1}) = \frac{hM_6}{\Sigma_n} \quad [6]$$

$$\Sigma_n = \text{constant to make } P_{n+1} + 2Q_{n+1} + R_{n+1} = 1.$$

Note that in writing down [6], F [number of female offspring in Table 1(d)] is being assumed large, although F does not enter into [6] directly.

Stability of altruist and nonaltruist fixation

Given each of the model recursions corresponding to Cases 1–9, one may now analyze the obtained recursions [3], [4], [6], etc. for fixedpoints and fixedpoint stability. From the genetics it is obvious that (1,0,0) and (0,0,1) will be fixedpoints in all cases, corresponding respectively to *A* and *a* fixation [in haplodiploid cases, it is also necessary to specify male (*A*,*a*) gene frequencies = (1,0), respectively (0,1)]. The present report will focus exclusively on analyzing the stability of these specific fixedpoints, although the results of analyzing additional internal fixedpoints (polymorphism) will be briefly noted.

Table 2 reports the results of the stability analysis in the form of conditions that each of the two fixations be stable. In all cases the reverse inequality (>) gives a condition for fixation instability. To illustrate the derivation of Table 2, consider again Case 1, where the recursion is given by the derivation of Table 1, [3]. For altruist fixation, straightforward linearization about (0,0,1) leads directly to a recursion

$$Q_{n+1} = \left(\frac{S\left(\frac{1}{2}\right)}{A(1)}\right) Q_n \quad [7]$$

in the perturbed heterozygote frequency Q_n, from which the stability condition reported in Table 2 follows at once. Stability analysis of the nonaltruist fixation is more difficult, since linearization of [3] about (1,0,0) degenerates. Notice, however, that selection in the neighborhood of (1,0,0) will be extremely slow. One may use this slow selection to approxi-

Table 3. Axioms used to establish implication orderings in Figs. 1 and 2

1. MS: $\beta > \beta' \Rightarrow S(\beta) > S(\beta')$ (strict monotonicity of $S(\beta)$);
2. ConS: $S(\beta)$ is convex downward ($\lambda_1, \lambda_2 \geqslant 0, \lambda_1 + \lambda_2 = 1 \Rightarrow \lambda_1 S(\beta) + \lambda_2 S(\beta') \leqslant S(\lambda_1\beta + \lambda_2\beta')$);
3. MA: $\beta > \beta' \Rightarrow A(\beta) > A(\beta')$ (strict monotonicity of $A(\beta)$);
4. Ord: $S(\beta) \geqslant A(\beta)$ for all β in [0, 1] (expected nonaltruist fitness is not less than expected altruist fitness);
5. WSCAL: $A(\beta) = (1 - \epsilon[\beta])S(\beta)$, where $\epsilon(\beta)$ is in (0, 1) for all β in [0, 1] and $\beta > \beta' \Rightarrow \epsilon(\beta) \geqslant \epsilon(\beta')$.

Note WSCAL $\Rightarrow$ Ord.

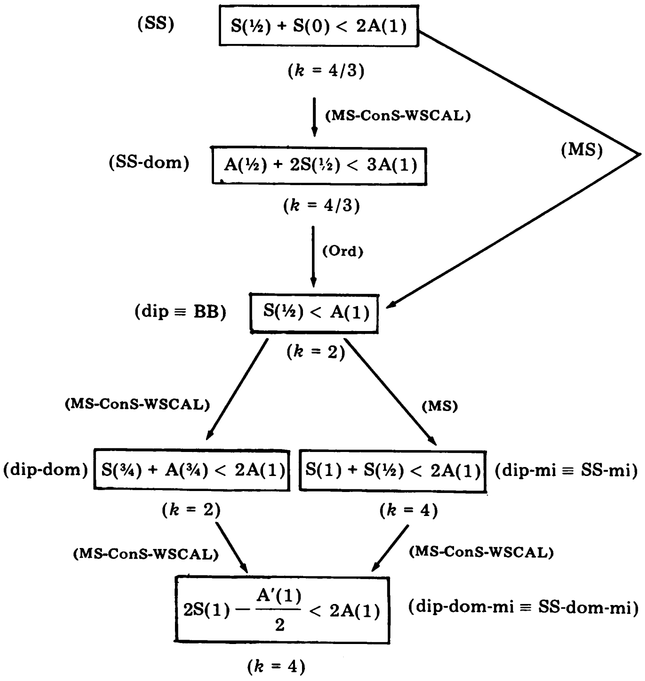

FIG. 1. Implication ordering of altruist stability conditions in general $A(\beta)$-$S(\beta)$ models under Table 3 axioms. Model abbreviations as in Table 2. One altruist stability condition A_1 is below a second condition A_2 iff $A_1 \Rightarrow A_2$. Axioms used to establish given implications are indicated; Hamilton k threshold is indicated for each model.

mate the mating frequency vector [2] by a new frequency vector

$$f_{HW} = (\xi_n^4, 4\xi_n^3\eta_n, 2\xi_n^2\eta_n^2, 4\xi_n^2\eta_n^2, 4\xi_n\eta_n^3, \eta_n^4), \qquad [2']$$

which amounts to the approximation that no selection at all is taking place and hence genotype frequencies are in their zygotic Hardy–Weinberg proportions. Using [2′] instead of [2], one obtains a simple one-dimensional recursion of the form $\eta_{n+1} = \phi(\eta_n)$, where η_n is the frequency of the altruist gene. Surprisingly, this new recursion can be shown to possess *exactly* the same stability condition for nonaltruist fixation as does the original recursion [3]†. Hence, the nonlinear stability of [3] about (1,0,0) can be given an exact analysis, which leads to the condition shown in Table 2.

Similar complications are encountered throughout Table 2 in analyzing the stability at fixation of dominant genes. In all cases, however, a similar procedure leads rigorously to exact stability conditions. In the haplodiploid Case 5, dominant stability analysis using [2′] leads to a recursion valid in the neighborhood of dominant fixation

$$\eta_{n+1} = \frac{1}{2}(\eta_n + \eta_{n-1}) + \left[\frac{2A\left(\frac{1}{2}\right) + S\left(\frac{1}{2}\right) - 3S(0)}{2S(0)}\right]\eta_n\eta_{n-1}, \qquad [8]$$

which may in turn be analyzed by a two-timing procedure,

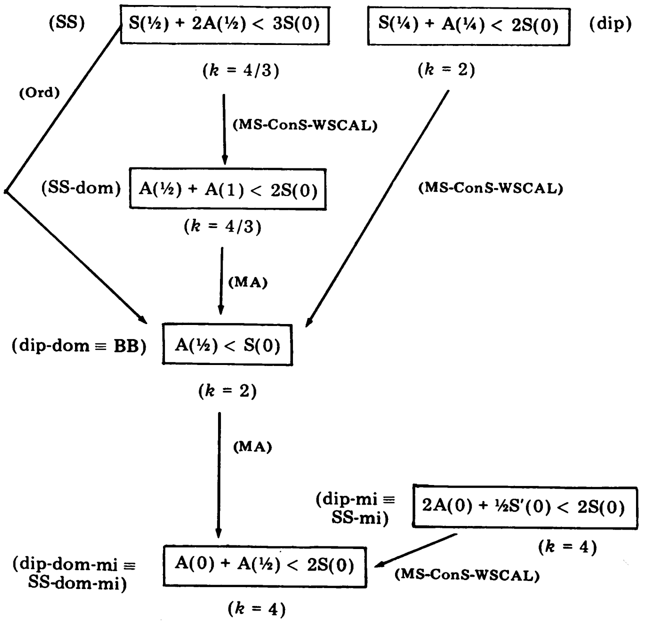

FIG. 2. Implication ordering of nonaltruist stability conditions. Details parallel to Fig. 1, but one condition S_1 is now placed below a second S_2 in the ordering iff $S_2 \Rightarrow S_1$. This enables the ordering to be read like Fig. 1 from top to bottom in order of models decreasingly favorable to the *altruist* trait.

leading finally to the result reported in Table 2.

It should be emphasized that all analysis upon which Table 2 is based is exact, and in particular involves no assumptions that kin selection pressure is weak.

Note also that many of the distinct cases in Table 2 lead to identical stability conditions.

Comparison of stability conditions

The next aim is to establish implications among the Table 2 conditions. It is obvious that this is a promising line of attack. For example, it is clear that stability of altruist fixation in Case 1 will imply stability of altruist fixation in Case 6, provided only that $S(\frac{1}{2}) \geq S(0)$. Hence, under this very weak provision Case 6 emerges as being at least as favorable to stable altruist fixation as Case 1, and in fact more favorable if $S(\frac{1}{2}) > S(0)$.

From a more systematic standpoint we now investigate the presence of similar implications among other pairs of stability conditions in Table 2.

Specifically, Table 3 introduces a set of axioms which restrict the form of $S(\beta)$ and $A(\beta)$ and which are used to establish the implications in Figs. 1 and 2. The strongest two axioms are clearly ConS, which imposes downward convexity on $S(\beta)$, and WSCAL, which asserts that the ratio $[S(\beta)/A(\beta)]$ is greater than 1 and increasing with β. If one thinks of nonaltruists as "cheaters" (using the terminology of ref. 12), i.e., as individuals who accept support from the altruists but who do not reciprocate in kind, then WSCAL asserts that it pays more to be a cheater the higher is the altruist fraction within the sibship, where the fitness of a "cheater" is computed relative to that of an altruist as a fixed scale unit.

A specific combinatorial model of fitness assignment, starting with the assumption that each altruist elects at random to support exactly one other sib has been developed†. This model, whose details will be reported elsewhere, leads to the specific fitness functions

$$A(\beta) = (1 - \epsilon)S(\beta) = (1 - \epsilon)(1 - qe^{-y\beta}), \qquad [9]$$

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† Full developments contained in two unpublished manuscripts: "Technical Appendix" appended to GS-2689 Progress Report, Department of Sociology, Harvard University, April, 1974; "Mathematical Models of Kin Selection in Diploid and Haplodiploid Systems," Courant Institute of Mathematical Sciences, April, 1975.

with $\epsilon \equiv q\delta$, $0 < q, y, \delta < 1$. These functions satisfy the Table 3 axioms, and in particular satisfy WSCAL trivially.

Figs. 1 and 2 now report implications among the stability conditions of Table 2 which may be derived making use of the Table 3 axioms. The specific axioms used to establish implications vary depending on the case and are reported for each implication. Both orderings are presented so that one can read them from top to bottom in an order of models progressively less favorable to the altruist trait. The following conclusions emerge:

1. Use of the Table 3 axioms leads to a nearly linear ordering in the altruist case (Fig. 1). The nonaltruist case (Fig. 2) is less tractable, although a substantial number of implications can also be established here.

2. The axioms ConS and WSCAL are crucial for establishing most of the comparisons, a major exception being the linear subordering in Fig. 1 ($\text{dip-mi} \equiv \text{SS-mi} \Rightarrow \text{dip} \equiv \text{BB} \Rightarrow \text{SS}$) which establishes implications among the altruist stability conditions for *recessive* altruist traits using MS only.

3. The obtained orderings are consistent with the predictions of Hamilton based on [**1**], although they reveal substantial complications which Hamilton's approach misses. For easy comparison with Hamilton's [**1**], both altruist and nonaltruist stability conditions in Figs. 1 and 2 are reported with the corresponding Hamilton k threshold in parentheses. The Hamilton threshold is seen to be consistent with both implication orderings in a nonstrictly monotonic sense. By contrast to the present models, Hamilton's k does not discriminate Mendelian dominance cases, and moreover imposes comparability on distinct models in instances where such comparability is not a consequence of the present axioms.

4. In addition to providing the comparative information in Figs. 1 and 2, the Table 3 axioms have also been used to investigate polymorphism behavior of the models[†]. Using MS, ConS, and WSCAL, it can first of all be shown that the altruist and nonaltruist stability regions are nonoverlapping for all models, i.e., altruist and nonaltruist fixations can never simultaneously be stable. Using the Table 3 axioms and assuming weak selection ($|[S(\beta)/S(0)] - 1| \ll 1$, $|[A(\beta)/S(0)] - 1| \ll 1$), details of internal fixedpoint behavior have been investigated in Cases 1 and 6. In both Cases, the Table 3 axioms enable one to show that polymorphism is unique and stable when it exists and will exist when and only when both fixations are unstable. This excludes the kind of threshold behavior characteristic of reciprocal altruism models (13, 14) and suggests a basic difference between the structure of selection for a reciprocal altruist trait and that of selection for a sib altruist trait satisfying Table 3.

DISCUSSION

This paper has presented an axiomatic basis for comparing sib selection models, starting from a rigorous population genetic formulation of several such models. The approach through the $A(\beta)$-$S(\beta)$ fitness functions allows great generality in specifying the effects of altruism. The major limitation on the present family of models lies elsewhere, in the assumption of large sibships. Extension of theory to handle the case where sibships need not be large is one major area where further work is needed, especially for possible applications to the higher social vertebrates.

The central payoff from the present reworking of sib selection theory lies only partly in the actual implication orderings shown in Figs. 1 and 2. Much additional information is contained in the particular axioms used to derive these orderings. These axioms suggest several new areas for substantive thinking, such as detailing what kind of "free-ride" nonaltruists may receive from a given kind of altruist activity, i.e., specifying the structure of $S(\beta)$. For investigating the monotonicity axioms MS and MA, fertility data such as that reported in refs. 8 and 15 may be relevant. The Table 3 axioms also suggest ties to economic theory, specifically through the role of convexity (ConS) [although it should be noted that in using ConS we have presently made use only of a very limited finite set of instances of the axiom, as it applies to the relations among $S(0)$, $S(\tfrac{1}{4})$, $S(\tfrac{1}{2})$, etc.; this is in contrast to typical uses of convexity assumptions in economic theory (16)]. The present theory appears to require presence of both ConS and WSCAL for well-behaved results: if either axiom is violated, then virtually any ordering of models becomes possible. This last fact need not, of course, necessarily refute Hamilton's basic Hymenopteran conjecture. In particular, it should be noticed that one can easily construct cases where ConS is violated which exhibit the following behavior: altruist fixation in a multiple insemination model (e.g., Case 3) is stable, but altruist fixation in the corresponding single insemination model (e.g., Case 1) is *unstable*. This type of possibility, which is *not* consistent with predictions derived from [**1**], suggests a new way that Hamilton's substantive conjecture may be consistent with instances where multiple insemination is in fact a characteristic of various Hymenopteran species (3, 17).

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