

COEFFICIENTS OF RELATIONSHIP AND COEFFICIENTS OF RELATEDNESS IN
KIN SELECTION: A COVARIANCE FORM FOR THE RHO FORMULA

by

M. Orlove and C. L. Wood

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ABSTRACT

Hamilton used the coefficient of relationship to predict the direction of selection acting on "genes for altruism" in a theoretical model. The sense (direction) of the inequality determined the direction of selection. But, paradoxically, Hamilton pointed out that traditional formulae for the coefficient of relationship cannot be evaluated during directional selection. Hamilton escaped the paradox by assuming very weak selection which could be treated like non-directional selection.

Later papers, including two by Hamilton, used other coefficients in place of the coefficient of relationship in the inequality. Thus inbreeding and directional selection could be handled in exact models. This paper tries to clarify the differences between the various coefficients and to point out an error in one of the author's previous work: Namely to state that there is analytical proof that the regression coefficient is a special case of a coefficient called \mathcal{P} whereas the earlier paper claimed only numerical verification was possible.

Since the symbol " \mathcal{P} " is also used to denote the correlation coefficient, it is suggested here that the \mathcal{P} of kin selection be given a new name.

Hamilton (1964 a,b) stated that altruism will be selected for if $K > 1/r$ and selected against if $K < 1/r$, where:

$$K = \frac{\text{Gain in beneficiary's Darwinian fitness}}{\text{Loss in altruist's Darwinian fitness}} \quad (1)$$

and r is the coefficient of relationship (fraction of genes identical by descent) between them. If we tag a small (almost zero), random fraction of altruism genes in a simulated population, then;

$$r = \text{PROB} \left(\begin{array}{l} \text{potential altruist} \\ \text{has tagged gene} \end{array} \mid \begin{array}{l} \text{potential beneficiary} \\ \text{has a tagged gene too} \end{array} \right). \quad (2)$$

There are exceptions to Hamilton's K - r rule so other coefficients have been used in place of r in Hamilton's inequality, q.v. B , the regression coefficient of relatedness. (Hamilton 1971, 1972, 1975; Orlove 1975 a,b). Hamilton chose the term relatedness to distinguish B from r , the coefficient of relationship. However recently Dawkins (1976 p98) ignored this distinction. When B was used in place of r in Hamilton's inequalities fewer exceptions occurred. To deal with these exceptions another coefficient, called \mathcal{P} , was used in place of r in Hamilton's inequalities (Orlove 1975 a,b). \mathcal{P} was defined such that no exceptions could occur.

The symbol " \mathcal{P} " was chosen because it is the Greek counterpart of the letter "r". The symbol " \mathcal{P} " is also used to denote the correlation coefficient. This is regrettable since whenever mating is random, the correlation coefficient is equivalent to B . It is hoped that the \mathcal{P} of kin selection be given a new name. Here no new name occurs. . . " \mathcal{P} " will be used for the new coefficient, and the correlation coefficient will be referred to by name as "the correlation coefficient". During polymorphisms maintained at a constant frequency, the correlation coefficient, B , and \mathcal{P} are equivalent. But if the frequency is intermediate, they deviate from r (contrary to popular belief).

In spite of these popular beliefs r and the correlation coefficient are not equivalent at intermediate frequencies even though the

population is in Hardy-Weinberg equilibrium at the time of zygote formation except for the special case of a neutral equilibrium existing simultaneously with codominance. This is because of an effective departure from Hardy-Weinberg equilibrium at the time of gamete production due to heterozygote advantage or homozygote advantage. For example, if two sibs have a homozygous parent, there is a 50% probability they will receive genes from that parent which are alike in state (but not identical by descent). This will increase the correlation coefficient but will not increase r . For non-directional selection the stability or instability is determined by the slope of the curve, P as a function of gene frequency, at the point where the curve intersects the horizontal line whose equation is $P = 1/K$, see Fig. 1. Concave-up curves show heterozygote advantage. Concave-down curves show homozygote advantage. Unlike classical (personal-fitness) models, the stability of polymorphisms in the kin selection model is not determined by heterozygote advantage or homozygote advantage. (Orlove 1975a). These results are easily accepted if we realize that the fitnesses of the diploid zygotes are frequency dependent.

We can consider each potential altruist and its potential beneficiary as a temporary "colony" comprised of 2 individuals.

Representing each colony as a point on a graph (see Orlove 1975 a):

Let N = the total number of points in the population

Let X_i = the X-coordinate of the i th point, i.e. the fraction of its genes that are altruism genes in the i th potential altruist.

Let Y_i = the Y-coordinate of the i th point, i.e. the fraction of its genes which are altruism genes in the i th potential beneficiary.

B is the slope of the best-fitting straight line (the regression line) through the cluster of N points, as determined by the least-squares method. This gives:

$$B = \frac{\sum_{i=1}^N X_i Y_i - \sum_{i=1}^N X_i \sum_{i=1}^N Y_i / N}{\sum_{i=1}^N X_i X_i - \sum_{i=1}^N X_i \sum_{i=1}^N X_i / N} \quad (3)$$

which becomes:

$$B = \frac{\text{COV} (X, Y)}{\text{COV} (X, X)} \quad (4)$$

(It will become apparent why explicit representation of 2nd degree terms and variance is being avoided.)

$\mathcal{P} = B$ except when there is: 1.) directional selection, 2.) a lack of codominance, and 3.) sex-limited selection, acting on the altruism gene. All 3 factors must exist simultaneously for \mathcal{P} not to be equivalent to B. (Orlove 1975 a,b). The second of these 2 papers stated that the equivalence of \mathcal{P} and B during codominance can be demonstrated numerically, but not analytically. This is in error and below follows a proof that $\mathcal{P} = B$ during codominance.

Let $F(Z)$ = the phenotype of a potential altruist with the fraction, Z , of its genes as altruism alleles, i.e. the fraction of its resources used selfishly.

Let $G(Z)$ = the "genotype" of an animal with the fraction, Z , of its genes as altruism alleles, i.e. the fraction of its gametes carrying the selfishness gene.

Then for the genotypes:

	AA	AS	SS	
$Z =$	1	1/2	0	
$G(Z) =$	0	1/2	1	FOR MENDELIAN SEGREGATION
$F(Z) =$	0	1/2	1	FOR CODOMINANCE
$F(Z) =$	0	0	1	FOR ALTRUISM DOMINANT

and so on.

Let X and Y take on the significance they did in the discussion on regression above. Then the regression of the genotype of the potential altruist on the genotype of the potential beneficiary is:

$$B = \frac{\text{COV} (G (X), G (Y))}{\text{COV} (G (X), G (X))} \quad (5)$$

The regression of the phenotype of the potential beneficiary on the genotype of the potential altruist is:

$$B = \frac{\text{COV} (G (X), F (Y))}{\text{COV} (G (X), G (X))} \quad (6)$$

and we shall see:

$$P = \frac{\text{COV} (G (X), F (Y))}{\text{COV} (G (X), F (X))} \quad (7)$$

When there is codominance: (and Mendelian segregation) $F=G$ and $P = B$.

Animal breeders evaluating the worthiness of bulls and roosters in programs to improve milk and egg production, consider directional selection on sex-limited characters exhibiting dominance. Should the breeders be criticized for using B instead of P in their calculations? Since they use only the numerators of the regression coefficients in their calculations involving the "A matrix" (Wright 1922; Henderson 1976), P and B give identical results so long as the regression is phenotype on genotype or genotype on phenotype (These last 2 regressions are equivalent if for every X^0, Y^0 colony there is an Y^0, X^0 colony. This is a safe assumption to make (Orlove 1975 a)).

This is so because under these circumstances P and B have identical numerators.

A P P E N D I X

(to derive the formula for \hat{p} , appearing in equation (7), which looks like the regression formula.)

Let X, Y, and N have the same meaning as above.

As above and in Orlove (1975a) let us assume that for every X^0, Y^0 colony there is one Y^0, X^0 colony.

As in Orlove(1975 a,b):

Let W=the number of offspring produced by a completely selfish potential altruist.

Let 0 (zero) = the number of offspring produced by a completely altruistic potential altruist.

Let Q_1 = the number of offspring produced by an unaided potential beneficiary.

Let $Q_1 + Q_2$ = the number of offspring produced by a completely-aided potential beneficiary.

Hamilton's $K = Q_2 / W$. The W is for worker and the Q is for queen.

Let q' =the frequency of the selfishness allele in the gametes entering next generation, i.e. produced in this generation.

$$q' = \frac{W \sum_{i=1}^N F(X_i)G(X_i) + Q_1 \sum_{i=1}^N G(X_i) + Q_2 \sum_{i=1}^N (1-F(Y_i)) G(X_i)}{W \sum_{i=1}^N F(X_i) + Q_1 \sum_{i=1}^N 1 + Q_2 \sum_{i=1}^N (1-F(Y_i))} \quad (8)$$

There are two ways to make the altruism allele and the selfishness allele equally fit.

- 1.) A cessation of selection, e.g. $W=0, Q_1=1, Q_2=0$, and
- 2.) non-directional selection, i.e. $W=p, Q_1=$ anything, $Q_2=1$.

If values of $0 < W < 1$ bother you, just imagine W , Q_1 , and Q_2 , each multiplied by the same arbitrarily-large constant. The constant cancels out in the formulae.

$$(W, Q_1, Q_2) = (0, 1, 0)$$

(9)

$$q' = \frac{\sum_{i=1}^N G(X_i)}{N}$$

$$(W, Q_1, Q_2) = (\rho, Q_1, 1)$$

(10)

$$q' = \frac{\rho \sum_{i=1}^N F(X_i)G(X_i) + Q_1 \sum_{i=1}^N G(X_i) + \sum_{i=1}^N (1-F(Y_i))G(X_i)}{\rho \sum_{i=1}^N F(X_i) + Q_1 \sum_{i=1}^N 1 + \sum_{i=1}^N (1-F(Y_i))}$$

Scudo and Ghiselin (197) obtained $\rho = r$ because they did the equivalent of assuming $Q_1/Q_2 = \text{infinity}$ in Equation (8)..

$$\frac{\sum_{i=1}^N G(X_i)}{N} = \frac{\rho \sum_{i=1}^N F(X_i)G(X_i) + Q_1 \sum_{i=1}^N G(X_i) + \sum_{i=1}^N (1-F(Y_i))G(X_i)}{\rho \sum_{i=1}^N F(X_i) + Q_1 N + \sum_{i=1}^N (1-F(Y_i))} \quad (11)$$

The philosophy justifying Equation (11) is discussed at length in Orlove (1977)

$$\begin{aligned} & \rho \sum_{i=1}^N F(X_i) \frac{\sum_{i=1}^N G(X_i)}{N} + Q_1 \sum_{i=1}^N G(X_i) + \sum_{i=1}^N (1-F(Y_i)) \frac{\sum_{i=1}^N G(X_i)}{N} \\ = & \rho \sum_{i=1}^N F(X_i)G(X_i) + Q_1 \sum_{i=1}^N G(X_i) + \sum_{i=1}^N (1-F(Y_i))G(X_i) \end{aligned} \quad (12)$$

The Q_1 terms cancel.

(13)

$$\begin{aligned}
& P \sum_{i=1}^N F(X_i)G(X_i) - P \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N \\
= & \sum_{i=1}^N (1-F(Y_i)) \sum_{i=1}^N G(X_i)/N - \sum_{i=1}^N (1-F(Y_i))G(X_i)
\end{aligned}$$

(14)

$$\begin{aligned}
& P \left(\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N \right) \\
= & \sum_{i=1}^N (1-F(Y_i)) \sum_{i=1}^N G(X_i)/N - \sum_{i=1}^N (1-F(Y_i))G(X_i)
\end{aligned}$$

(15)

$$\begin{aligned}
P = & \frac{\sum_{i=1}^N (1-F(Y_i)) \sum_{i=1}^N G(X_i)/N - \sum_{i=1}^N (1-F(Y_i))G(X_i)}{\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N}
\end{aligned}$$

Here are two identities we need.

* * * * *

(16)

$$\sum_{i=1}^N (1-F(Y_i)) = N - \sum_{i=1}^N F(Y_i)$$

(17)

$$\sum_{i=1}^N (1-F(Y_i))G(X_i) = \sum_{i=1}^N G(X_i) - \sum_{i=1}^N F(Y_i)G(X_i)$$

* * * * *

(18)

$$\rho = \frac{(\sum_{i=1}^N F(Y_i)) \sum_{i=1}^N G(X_i)/N - (\sum_{i=1}^N G(X_i) - \sum_{i=1}^N F(Y_i)G(X_i))}{\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N}$$

$$\rho = \frac{\sum_{i=1}^N G(X_i) - \sum_{i=1}^N F(Y_i) \sum_{i=1}^N G(X_i)/N - \sum_{i=1}^N G(X_i) + \sum_{i=1}^N F(Y_i)G(X_i)}{\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N} \quad (19)$$

$$\rho = \frac{\sum_{i=1}^N F(Y_i)G(X_i) - \sum_{i=1}^N F(Y_i) \sum_{i=1}^N G(X_i)/N}{\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N} \quad (20)$$

$$\rho = \frac{\sum_{i=1}^N F(Y_i)G(X_i) - \sum_{i=1}^N F(Y_i) \sum_{i=1}^N G(X_i)/N}{\sum_{i=1}^N F(X_i)G(X_i) - \sum_{i=1}^N F(X_i) \sum_{i=1}^N G(X_i)/N}$$

$$\rho = \frac{\text{COV}(G(X), F(Y))}{\text{COV}(G(X), F(X))} \quad (21)$$

which, in the notation of Orlove, (1975b) becomes

$$\rho = \frac{\text{COV}(I \frac{1}{2} J, J \supset K)}{\text{COV}(I \frac{1}{2} J, I \supset J)} \quad (22)$$

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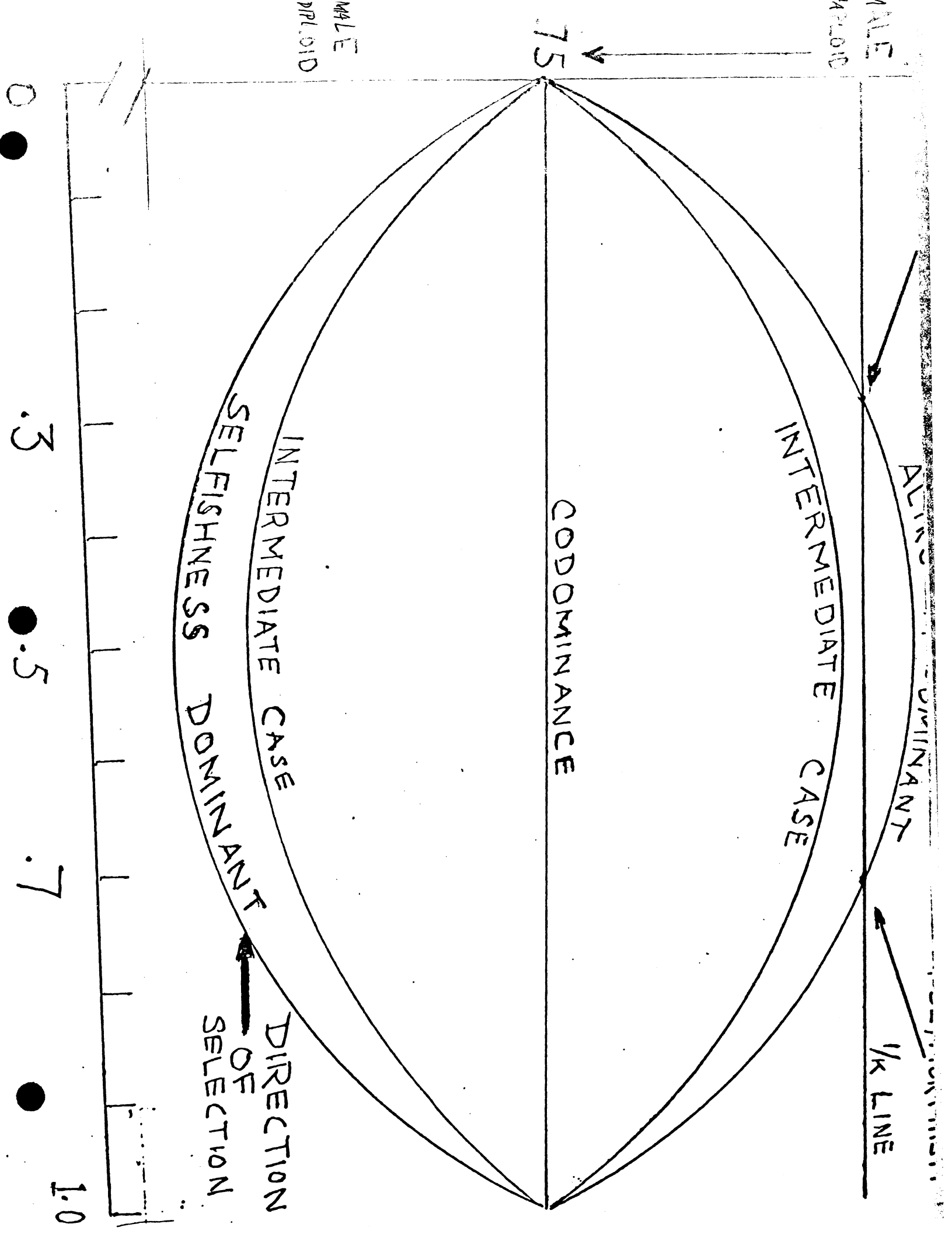
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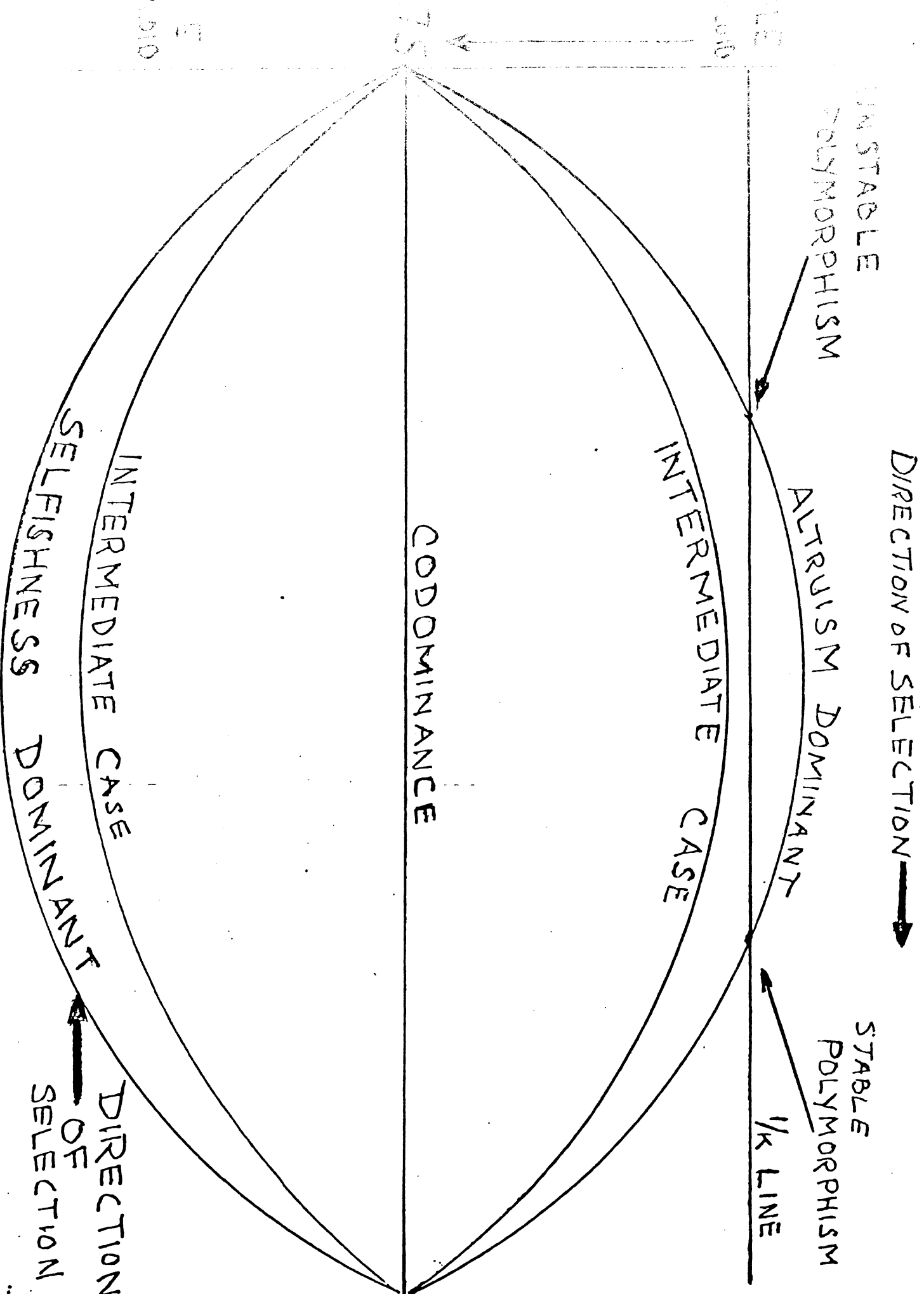
Fig. 1 STABILITY OF POLYMORPHISMS IN ALTRUISM AMONG SIBLINGS

If the $1/K$ line is in view on this graph, then the population will be confined to the immediate proximity of one of the curves. It will move along the curve in ^{the} direction indicated by the arrow on the same side of the $1/K$ line as the population. If the $1/K$ line doesn't intersect the curve, then fixation results. The drawing is schematic: the selfishness-dominant curve has a minimum which is slightly further from the codominance line than the maximum of the altruism-dominant curve; all the maxima and minima occur at frequencies of the altruism gene slightly less than .5; the maxima and minima are never more than a distance of .03 from the codominance line. The correlation coefficient, B , and \bar{P} are, for all practical purposes, equivalent when the $1/K$ line intersects one of these curves. r remains on the line labeled "CODOMINANCE" during all degrees of dominance, except in the case where the altruism gene was rare when the initial mutation event, simulated by the "tagging" (see equation (2)), occurred. However, \bar{P} is on the codominance line only during codominance.

Adapted from Orlove (1975a).

NOTE TO THE EDITOR: Horizontal axis should be labeled "FREQUENCY OF ALTRUISM GENE". Vertical axis should be labeled " \bar{P} ".





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