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The American Naturalist, Vol. 114, No. 5 (Nov., 1979), 637-647.

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MEASURES OF GENETIC RELATIONSHIP AND THE CONCEPT OF INCLUSIVE FITNESS

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Submitted November 22, 1977; Accepted June 2, 1978

The concept of inclusive fitness lies at the heart of most sociobiological arguments. This concept recognizes that an individual's fitness includes the effects the individual has upon the fitnesses of relatives, these effects being weighted by some measure of the degree of genetic relationship. Consequently, the traditional unit of natural selection, the individual, is extended. Genes were once pictured as packaged discretely at the individual level. However, the concept of inclusive fitness dissolves this barrier and replaces it with a genetic gradient of decreasing identity. The proper genetic unit perceived by natural selection must now be decided on a case by case basis using information concerning social structure, population structure, and genetic relationships.

It is obvious that this concept remains inoperative unless provided with an appropriate measure of the degree of genetic relationship. Our purpose in this report is (i) to briefly review and compare some measures which have been utilized in the literature, (ii) to develop from traditional population genetic theory a measure which we feel fits the needs of sociobiology, and (iii) to see what implications this measure has for the theory of evolution by kin selection. Before proceeding we would like to mention a different approach which has been widely used in this area.

Selection models based on gene frequency changes have been especially useful in exploring the evolution of social behavior by kin selection. Within explicitly specified contexts of interaction (e.g., sib-sib relations), it is possible to model changes in gene frequency without any explicit reference to a measure of genetic relationship (see, for example, Orlove 1975; Charnov 1977; Charlesworth 1978; Cavalli-Sforza and Feldman 1978; Michod 1979). However, in this approach the genetic context of selection on the altruistic gene is specified, and consequently knowledge of the genetic relationship is implicitly assumed. There is no doubt in our minds that this approach is more direct and that questions concerning the establishment of altruistic genes can best be answered by these means. In this regard, it is possible to incorporate the probability approach discussed later into a

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model of gene frequency change and to show that the resulting condition for spread of the altruistic gene involves the very coefficients derived in this paper: equations (6) below (Michod 1979, eq. [3]). However, with one eye toward the practicing sociobiologist, our concern here is more with operationalizing the theory of kin selection. In other words, in testing the theory, how should a researcher presented with a population of organisms of known pedigree measure genetic relationships?

It must be stressed that the coefficients discussed in this paper, with the exception of Orlove's ρ (Orlove 1975; Orlove and Wood 1978), are static measures of genetic relationship and are not intended to cope with the dynamical aspects of selection. Consequently their application in the theory of kin selection implicitly assumes that selection is weak (see Michod 1979).

COEFFICIENTS OF RELATIONSHIP AND RELATEDNESS

Wilson (1975, pp. 74, 118) and Hamilton (1964) initiate their discussions of kin selection by using Wright's (1922) "coefficient of relationship," r_{XY} . The coefficient r_{XY} is defined to be the theoretical correlation between relatives X and Y for some quantitative trait, assuming additivity of gene effects both between different loci and between different alleles at each locus (i.e., heterozygotes intermediate). Let f_X and f_Y be the inbreeding coefficients of individuals X and Y , and let f_{XY} be the correlation between gametes, one taken from X and one from Y . In other words, f_{XY} is the inbreeding coefficient of a hypothetical offspring of X and Y ; f_{XY} has had a variety of names in the literature, including "coefficient of kinship" (Jacquard 1974), "coefficient of coancestry" (Malécot 1969), and "coefficient of consanguinity" (Crow and Kimura 1970). The coefficient of relationship can be defined in terms of pedigree information (Wright 1922; Crow and Kimura 1970, p. 138):

$$r_{XY} = \frac{2f_{XY}}{[(1 + f_X)(1 + f_Y)]^{1/2}} = \frac{\sigma_{XY}^2}{\sigma_X \sigma_Y} \quad (1)$$

where σ_{XY}^2 and σ_X^2 , σ_Y^2 indicate the genotypic covariances and variances between and within individuals X and Y for the trait under examination. In the theory of kin selection the coefficient r_{XY} has been interpreted as the fraction of genes shared by X and Y (Wilson 1975, p. 74; Orlove 1975; Orlove and Wood 1978; Crow and Kimura 1970, pp. 67, 244, 489). For a discussion of the use of r_{XY} in haplodiploid genetic systems, see Crozier (1970).

Hamilton (1971, p. 76; 1972, p. 195) defines the "coefficient of relatedness" b_{YX} as the corresponding regression coefficient for Y on X :

$$b_{YX} = \frac{2f_{XY}}{1 + f_X} = \frac{\sigma_{XY}^2}{\sigma_X^2}. \quad (2)$$

Hamilton denoted this coefficient as b_{XY} , but we use b_{YX} to be consistent with conventional statistical notation. Obviously $r_{XY} = b_{YX}$ if $f_X = f_Y$, or if $\sigma_X^2 = \sigma_Y^2$, which is less restrictive. One use of b_{YX} in kinship theory lies in its interpretation

as the fraction of genes carried by X which can be expected to occur as replicas in Y (Hamilton 1971, p. 70; Orlove and Wood 1978).

It is obvious that r_{XY} and b_{YX} convey much the same information, as they are related by the formula

$$b_{YX} = r_{XY} \frac{\sigma_Y}{\sigma_X}. \quad (3)$$

The genotypic variance of an individual X with inbreeding f_X , assuming only additive effects at all loci, is well known to be (Crow and Kimura 1970):

$$\sigma_X^2 = (1 + f_X)\sigma_A^2, \quad (4)$$

where σ_A^2 is the additive genetic variance for loci determining the trait in the population containing X and Y . The genotypic covariance between X and Y for completely additive gene action when X and/or Y may or may not be inbred is $\sigma_{XY}^2 = 2f_{XY}\sigma_A^2$. The corresponding formulae between inbred individuals with epistatic interactions between loci and dominance deviations at loci are much more complex. Formulae for the variance and covariances in these cases, as well as others, are given in Harris (1964; eq. [4] follows from his eq. [25] under the stated simplifying assumptions).

The coefficient ρ developed in Orlove and Wood (1978) is very similar to the coefficients above, though Orlove's perspective is somewhat different. The basic data from which ρ is developed are the fractions of altruistic genes themselves. This presents no problem for theoretical discussions, but for applications this limitation is considerable. Orlove's ρ is defined to be

$$\rho = \frac{\text{Cov}[G(X), F(Y)]}{\text{Cov}[G(X), F(X)]}$$

where G and F denote genotype and phenotype, respectively. When there is codominance and $F = G$, $\rho = b$ (Orlove and Wood 1978), so long as b is modified for possible differences in gene number between males and females, as in haplodiploid genetic systems.

The covariance of genotype and phenotype in ρ is meant to handle dominance and not environmental or developmental effects. However, as is also true of all the above coefficients, there is no reason why these additional factors could not be included. Wright's usage of path analysis in determining r_{XY} is explicitly formulated to cope with the effects of dominance, environment, and development (Wright 1921a, 1921b).

Comparison of r_{XY} and b_{YX} for Haplodiploidy

We now calculate and compare r_{XY} and b_{YX} for parent-offspring relations in haplodiploid genetic systems by Wright's technique of path coefficients (Wright 1934). A good reference for path analysis is Li (1976, chaps. 14–16; 1975). The path diagram and definitions are given in figure 1. Unless indicated to the contrary in figure 1, the path coefficients are $a^2 = .5/(1 + f)$ and $b^2 = .5(1 + f)$ while $m = f/b$.

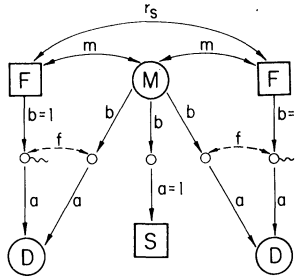


FIG. 1.—Path diagram of parent-offspring relations for haplodiploid genetic systems; F = fathers, M = mother, D = daughters, S = son, r_s = correlation between random sperms in spermatheca of female (Hamilton 1972), f = correlation between uniting gametes, m = correlation between genetic constitution of parents, a = path coefficient from gamete to zygote, b = path coefficient from zygote to gamete.

The inbreeding coefficient f is assumed constant for simplicity. By the theory of path analysis, the correlation between any two individuals is equal to the sum of all paths connecting them (see Li 1976, p. 270 for the rules used in tracing paths). By these rules the following coefficients of relationship can be calculated: $r_{MS} = [(1+f)/2]^{1/2}$, $r_{MD} = (1+3f)/[2(1+f)]$, $r_{DD} = (1+5f+2r_s)/[4(1+f)]$, $r_{SS} = (1+f)/2$, $r_{DS} = (1+3f)/[8(1+f)]^{1/2}$, $r_{FD} = (1+f)/[2(1+f)]^{1/2}$, $r_{FS} = f$. With the genetic variance of females given in (4) and that of haploid males equal to $\sigma_A^2/2$, the corresponding coefficients of relatedness (the regression coefficients) can be calculated by formula (3) to be: $b_{DD} = r_{DD}$, $b_{MD} = b_{DM} = r_{MD}$, $b_{FS} = b_{SF} = r_{FS}$, $b_{SS} = r_{SS}$, $b_{SM} = \frac{1}{2}$, $b_{MS} = 1+f$, $b_{DS} = (1+3f)/2$, $b_{SD} = (1+3f)/[4(1+3f)]$, $b_{DF} = 1+f$, $b_{FD} = \frac{1}{2}$. These values are equivalent to those of Hamilton (1972, table 2) if the sex-ratio is equal. However, note that these values correspond to what Hamilton termed the “complete” or “life-for-life” coefficients of relatedness, B (1972, p. 203), and not the coefficient defined by his equation (1) (1972, p. 195). For example, by this formula $b_{SM} = 1$ instead of .5 as given above. According to this definition b_{YX} equals the probability with which a random gamete of Y carries of particular allele of X divided by the probability with which a random gamete of X carries the allele. However, this definition does not take into account the differences in gene number between males and females and the concomitant differences in genetic variances. As shown above, and also noted by Hamilton (personal communication), the formal regression of Y 's genotype on X does. A similar regression analysis was used by Wright (1932, 1977, pp. 230–233) in selecting for improved milk production of dairy cattle. For a trait, like milk production, which is expressed only in females, the selection of males for breeding can be made on the basis of milk production of close female relatives. The selection of males based on these regression estimates from female relatives is remarkably similar to the modern notion of kin selection.

Limitations

One of our goals is to point out limitations of r_{XY} and b_{YX} for use in calculations of inclusive fitness. The interpretation of correlation and regression coefficients as

fractions of causative factors (genes in this case) shared requires that the independent factors be identical in variability and effect. In the case of genes, these are very restrictive conditions and require identical gene effects and identical allele frequency arrays across loci, in addition to total additivity. In S. Wright's (personal communication) words: "Even if the factors are all equivalent in effect, it is unlikely that the frequency arrays of the loci would be the same. Even if the same in a random breeding population ($f = 0$), they would not remain the same under inbreeding. There would be a stochastic distribution with varying approaches to fixation among the loci with inbreeding. Thus the interpretation of the coefficient of relationship as the proportion of common factors has little concrete meaning and this is especially the case if there is inbreeding."

To apply these coefficients in the absence of pedigree information it is necessary to know the various contributions of genotype, dominance, environment, and development to the phenotype. Even if these components are estimated, the restrictive conditions just indicated must hold for the interpretation of these coefficients as fractions of genes shared. If pedigree information is available an exact coefficient can be calculated, as we show in the next section.

What is the appropriate measure of the degree of genetic relationship between two individuals for use in the theory of kin selection? In the next section we construct a framework which we feel clarifies some of the issues involved.

PROBABILITY APPROACH

In this section we abandon the statistical approach of the previous section and develop a probability coefficient which exactly measures "the conditional probability that a second individual (Y) has a given gene if a related individual (X) is known to have the gene" (Trivers and Hare 1976, p. 249). It is this conditional probability which Hamilton's theory requires (Charnov 1977; Cavalli-Sforza and Feldman 1978; Harpending 1979; Michod 1979). We ask, "Given genetic information of individual X , with what probability can we predict the alleles in a random gamete of Y ?"

Following Hamilton (1971, 1972) and Charnov (1977), we define this sociobiological problem in the context of a single diploid locus and then employ traditional inbreeding theory as a tool in clarifying the issues involved. Consider two individuals X and Y and their four alleles at a single locus. If no distinction is made concerning the parent from which each allele came (this distinction is unnecessary for our purposes), there are nine possible states of identity (otherwise there are fifteen). These states are diagrammed in figure 2. These nine events have probabilities: $\Delta_1, \Delta_2, \Delta_3, \Delta_4, \Delta_5, \Delta_6, \Delta_7, \Delta_8, \Delta_9$, which can be calculated from any pedigree by a variety of techniques (Harris 1964; Cockerham 1971; Denniston 1974; and others). The traditional two-allele coefficients of inbreeding, interpreted as probabilities, are:

$$\begin{aligned} f_X &= \Delta_1 + \Delta_2 + \Delta_3 + \Delta_4, & f_Y &= \Delta_1 + \Delta_2 + \Delta_5 + \Delta_6, \\ f_{XY} &= \Delta_1 + \frac{1}{2}(\Delta_3 + \Delta_5 + \Delta_7) + \frac{1}{4}\Delta_8. \end{aligned} \quad (5)$$

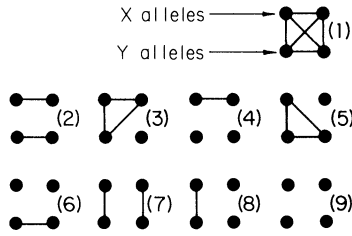


FIG. 2.—Nine possible states of identity between diploid individuals *X* and *Y*. Genetic identity between alleles is indicated by a connecting line.

In hopes of casting the problem in a proper setting, we use Jacquard's (1974) notion of "genetic structure." Let $s = (p_1, \dots, p_i, \dots, p_n)$ be the genic structure of the population or the vector of allele frequencies at the locus of consideration. Here p_i is the frequency of the i th allele in the population. Define the genic structure of individual *X* as the vector $s_X = (p_1, \dots, p_i, \dots, p_n)$ where now p_i is the probability that a gamete of *X* carries allele i . Define s_Y likewise. If *X* is heterozygous for alleles A_2 and A_4 , *Y* is homozygous for allele A_3 , and there are five alleles segregating at this locus, then $s_X = (0, .5, 0, .5, 0)$ and $s_Y = (0, 0, 1, 0, 0)$. In other words, the genic structure of an individual is the probability distribution of alleles in its gametes. The essence of evolutionary decisions based on kinship concerns the ability of *X* to predict the genic structure of *Y* at the locus of the hypothetical altruistic gene.

Taking the perspective of *X*, the appropriate conditional probability (conditioning on the genotype of *X*) is calculated by weighting the probabilities of the identity events in figure 2 by the information they provide (see Jacquard 1974, chap. 6, as corrected by Elston and Lange 1976);

$$s_{Y/A_i A_j} = \left(\frac{\Delta_5 + \Delta_7 + \frac{1}{2}\Delta_8}{1 - f_X} \right) s_X + \left(\frac{\frac{1}{2}\Delta_8 + \Delta_6 + \Delta_9}{1 - f_X} \right) s,$$

$$s_{Y/A_i A_i} = [u_i(\Delta_1 + \frac{1}{2}\Delta_3) + v_i(\Delta_5 + \Delta_7 + \frac{1}{2}\Delta_8)] s_X \tag{6}$$

$$+ [u_i(\Delta_2 + \frac{1}{2}\Delta_3 + \Delta_4) + v_i(\Delta_6 + \frac{1}{2}\Delta_8 + \Delta_9)] s,$$

where $u_i = 1/[p_i + (1 - p_i)f_X]$ and $v_i = p_i u_i$. Equations (6) above are Jacquard's (1974, sect. 2.3) equation (17) and the corrected version of his (18); see Elston and Lange (1976). These corrections and their motivation will appear in the forthcoming editions of Jacquard's book (A. Jacquard, personal communication). The probability with which *X* can predict the genic structure of *Y*, given that *X* is heterozygous, is $s_{Y/A_i A_j}$. Except that *X* is homozygous, $s_{Y/A_i A_i}$ is defined likewise. The first term on the right hand side (RHS) of both equations (6) contains a probability multiplied by the genic structure of *X*. This probability takes into account the pedigree ties which *X* has with *Y* and represents the probability with which *X* can predict the genic structure of *Y* on the basis of this information. It is exactly the conditional probability demanded above. It depends on the genotype of *X*, because if *X* is heterozygous events 1, 2, 3, and 4 cannot occur. It is important to note that if *X* is homozygous this first term depends upon gene

frequency, while this is not so if X is heterozygous. An explicit example will illustrate the importance of this fact in the next section. It is possible to form other probabilities by weighting the basic events in figure 2 in different ways. However, to keep the predictive nature of the argument one must condition on X . The second term on the RHS contains a probability multiplied by the genic structure of the population at large. This is the probability with which X can predict the genic structure of Y using the gene frequencies in the population as information instead of the pedigree ties. It can be taken or left according to one's purpose, as will be discussed subsequently. If X is not inbred (6) simplifies to $s_{Y/X} = 2f_{XY}s_X + (1 - 2f_{XY})s$, and consequently f_{XY} is a sufficient predictor of genetic relationships only when $f_X = 0$.

It is a simple matter to convince oneself that $2f_{XY}$ is exactly the fraction of genes shared, if X and Y are not inbred (e.g., see Wilson 1975, p. 75). In the case of no inbreeding, it can easily be seen that $2f_{XY} = r_{XY} = b_{YX}$ and so $s_{Y/X}$ becomes identical with these other coefficients. However, as Hamilton himself realized, "difficulties in the interpretation of genotypic inclusive fitness (also) remain in cases of inbreeding" (1972, p. 196). In retrospect it is clear why f_{XY} cannot properly assess the relationship between the genic structures of inbred individuals. If X is not inbred, knowledge of one allele at a locus provides no information about the other. However if X is inbred, the two alleles are no longer independent and information about one contains information about the other. By considering only one random allele from X , f_{XY} ignores this extra information.

DISCUSSION

The measure of genetic relationships given in (6) has several theoretical advantages. First, it exactly describes the ability of one individual to predict the genic structure (i.e., allelic distribution in gametes) of another individual in inbred situations. Second, it partitions this predictive power into a component due to pedigree ties and a component due to the population gene frequency. Third, it is very sensitive to best measure asymmetries in genetic relationship.

Population gene frequency can have important effects in the theory of kin selection. As realized by others (Hamilton 1971, 1972; Trivers and Hare 1976), it is clear that as populations become more homozygous (for whatever reason) the effect of identity due to pedigree ties becomes diluted. In organisms with small populations this effect could be substantial. As discussed by Hamilton (1971, appendix II), if populations were structured into small semi-isolated subpopulations for long periods of time random differentiation among subpopulations would occur. At the same time, genetic identity within each subpopulation would increase due to finite population size. Consequently, randomly chosen gametes within subpopulations would be correlated with respect to gametes randomly chosen from the population at large (as measured by Wright's [1951] f_{ST}). This identity would be reflected in the component of (6) due to population gene frequency.

In addition, suppose a gene determining social behavior (altruistic, spiteful, or selfish) also causes a noticeable effect on the phenotype, so that presence of the

gene can be recognized by other individuals. This recognizable phenotype could be produced as a pleiotropic effect. As Hamilton (1964, p. 54) points out, genes with similar effects are at the basis of the evolution of assortative mating. Social acts such as altruism could then be directed to individuals of the same phenotype, and such "signal" genes would enjoy a powerful selective advantage. An individual's inclusive fitness would include not only considerations of relatives, but also members of a broader phenotypic class sharing the same signal gene. Although this component of inclusive fitness would be small (i.e., sharing a single gene) relative to the large fractions of genes shared between relatives, it could exert a dominating effect on an individual's behavior. Admittedly, we can think of no example. However, if such situations occur, the component of genetic relationship due to population gene frequency would be very important.

We feel an important weakness of coefficients like r_{XY} and f_{XY} (though not always b_{YX}) for use in sociobiology is that they are symmetrical with respect to the individuals involved. Asymmetries in genetic relationship are fundamental to kin-selection arguments. The intrinsic asymmetries of haplodiploid genetic systems are thought to explain much of the evolution of Hymenopteran societies (Hamilton 1964, 1972). Also, in diploid genetic systems with inbreeding, asymmetric situations exist (e.g., events 3 and 5 in fig. 2) and it seems important to use a measure of genetic relationship which can discriminate such asymmetries. It is also an easy matter to construct pedigrees where the predictive power of the degree of genetic relationship as measured by (6) is different with respect to X and Y (i.e., $s_{X/A_iA_j} \neq s_{Y/A_iA_j}$, etc.). Indeed, X and Y could even be equivalent from the point of view of the pedigree, but with one individual homozygous and the other heterozygous. Consequently (by [6]) they would have different predictive capabilities (see calculations for fig. 3 below). If the basic events of fig. 2 were worked through for haplodiploid genetic systems, asymmetry would become crucial. No symmetrical measure can properly assess these situations.

The measure of the degree of genetic relationship given in (6) has certain practical difficulties. Although the theory of kin selection requires the conditional probability of Y having the altruistic gene, given that X has it (Hamilton 1972; Charnov 1977; Cavalli-Sforza and Feldman 1978; Harpending 1979; Michod 1979), in practice the researcher will not know the genotype of the individuals observed. However, if by the technique of gel electrophoresis one knew that a certain percentage of loci were heterozygous, it might be possible to weight the conditional probabilities in front of s_X in (6) to get a measure of identity across loci. Indeed, the appropriate weighting can be deduced from a model of gene frequency change (Michod, 1979, eq. [3]).

Equations (6) indicate that the conditional probability of Y having the altruistic gene(s) if X does, depends on the genotype of X . This means that the average relationship within a population of individuals depends upon genotype frequencies. If the gene is rare it is clear that it will most often be in heterozygous state. However, as the gene increases in frequency there could exist an equilibrium in the spread of altruism when the cost/benefit ratio (Hamilton 1972) is somewhere in between the most extreme values of s_{Y/A_iA_i} and s_{Y/A_iA_j} (Hamilton, personal communication). For the example below (fig. 3) this range would be .500–.667. Indeed,

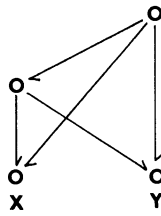


FIG. 3.—Illustrative pedigree; see text for explanation; *X* and *Y* are full sibs with parents who are themselves parent and offspring.

such frequency dependence is basic to recent population genetic models of kin selection (Charnov 1977; Cavalli-Sforza and Feldman 1978; Michod 1979).

For explicitness, consider the pedigree in figure 3. In this pedigree *X* and *Y* are offspring of a parent-sib mating. Such matings occur in termites when a king or queen dies and the worker castes rear a substitute from the eggs already present. This “neotene” then mates with the surviving parent. Calculation of the nine probabilities of figure 2 yields: $\Delta_1 = .0625$, $\Delta_2 = 0$, $\Delta_3 = \Delta_5 = .125$, $\Delta_4 = \Delta_6 = .0625$, $\Delta_7 = .1875$, $\Delta_8 = .375$, $\Delta_9 = 0$. Substituting these values into formulae (5) gives $f_X = f_Y = .25$, $f_{XY} = .375$; $r_{XY} = b_{XY} = b_{YX} = .6$ by (1) and (2); while from (6) we have

$$s_{Y/A_i A_j} = .6667s_X + .3333s$$

$$s_{Y/A_i A_i} = \frac{1}{6p_i + 2} [(1 + 4p_i)s_X + (1 + 2p_i)s]$$

which for

$$p_i \approx 0, \quad s_{Y/A_i A_i} = .500s_X + .500s;$$

$$p_i = \frac{1}{2}, \quad s_{Y/A_i A_i} = .600s_X + .400s;$$

$$p_i = 1, \quad s_{Y/A_i A_i} = .625s_X + .375s.$$

Consequently, the actual probability with which *X* can predict the degree of genetic relationship lies in the range .500–.667 and depends upon whether *X* is homozygous or heterozygous and the gene frequency. Depending on these considerations, the difference between $s_{Y/X}$ and r_{XY} or b_{YX} can reach 20%, for the simple pedigree in figure 3.

A difference between measures becomes important only to the degree that natural selection can act on it. The question becomes, to what degree? If natural selection cannot sense pedigree ties which make a 20% difference in the degree of genetic relationship, then, for the example above, the measures are operationally the same. It is not clear if our concern for the proper coefficient makes any difference in practice. Nevertheless, it seems important to appreciate the issues involved in constructing an exact measure even if the differences between measures are sometimes swamped out in nature.

SUMMARY

Measures of the degree of genetic relationship between individuals are discussed and compared from the viewpoint of the theory of kin selection. Lim-

itations of Wright's coefficient of relationship and Hamilton's coefficient of relatedness are discussed. Jacquard's theoretical framework of predicting genic structures is employed in hopes of clarifying the issues involved: (i) measuring genetic relationships between inbred individuals, (ii) the effect of population gene frequency, and (iii) measuring asymmetrical genetic relationships.

ACKNOWLEDGMENTS

We would like to thank Sewall Wright for corresponding with us on this problem, William D. Hamilton for his thoughtful criticism of a previous version of this paper, and Bob Abugov, Brian Charlesworth, Ross Crozier, Albert Jacquard, Chris Starr and Bruce Weir for discussion and comment.

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