Genetics and Molecular Biology, 23, 1, 49-51 (2000)

Short Communication

A new concept of relatedness and its significance to the theory of social evolution*

M.S. Drummond

Abstract

Data on primitively social groups of Hymenoptera have been somewhat contradictory with respect to kin recognition, degree of relatedness and social evolution. This study presents a new concept of "relatedness coefficient". Called "aggregated relatedness", the hypothesis here introduced proposes that genes shared by any two individuals affect formation of family units to an extent dependent on their frequency and manner of dispersion in neighboring populations.

INTRODUCTION

Relatedness, i.e., genetic similarity by descent, constitutes the basis of sociobiology theory (Hamilton, 1964). Although the significance of relatedness in this context is well founded based on Hamilton's rule, it is necessary to consider, apart from costs and benefits, whether only the genetic link between the altruist and the beneficiary would be necessary and sufficient for Hamilton's rule to be valid. Indeed, many situations exist in which relatedness is apparently the factor contribuing least to the stability of a social group (Bourke and Franks, 1995). In such cases, the balance between costs (*c*) and benefits (*b*) is invoked to explain the maintenance of social cohesion. These two parameters, however, are difficult (if not impossible) to measure. From this viewpoint, the sociobiology theory might be based on a parameter, relationship by descent, which may in fact constitute an artifact or a byproduct of another possibly more important unrecognized parameter, which could be the key to understanding sociality. This alternative concept, which I call aggregated relatedness, is dealt with in this study.

The aggregated relatedness hypothesis

Aggregated relatedness constitutes a new formulation for expressing genetic similarity among individuals in a population. It represents the degree of relationship based on the social value of a given characteristic, measured according to its relative weight in the population. This concept explains population structure based on relatedness, thus can evaluate the social predisposition of a given animal group.

Although relatedness estimation by means of regression establishes a link from individual *A* to *B*, what must be considered is the aggregated value of such a link as a function of the frequency of the genes in the population, i.e., pairs of individuals presenting genes infrequent in the population must have higher aggregated relatedness values than those individuals with more common genes. This means that alone the degree of genetic similarity between those individuals does not suffice but also how the population is structured in terms of distribution and frequency of the genes involved.

As an example, let us consider the situation in which a female *A* is equally related to α and β, her descendants (Figure 1). Each descendant carries half of the mother's genes. Among its maternal genes, β carries copies of a gene (a^y) which is very common in the population, whereas α carries a rare gene (a^x) which is as advantageous as its corresponding allele. In this case, the genetic similarity of β to *A*, regarding this locus, does not differ as much from the mean similarity of β to the population as a whole when compared to the difference from α to *A*. The mean similarity of *A* to the population is strongly influenced by only one of the alleles (the more abundant a^y) so that the similarity differential of $r_{\beta A}$ (read relatedness of β to *A*) and $r_{\alpha A}$ in relation to r_{Ap} (read relatedness of A to population) cannot be the same. In other words, for the above case, it can be said that the aggregated relatedness value of α to *A* is greater than the aggregated relatedness value of β to *A*, although both have the same relatedness value, i.e.,

$$\frac{r_{\beta A}}{r_{\beta p}} < \frac{r_{\alpha A}}{r_{\alpha p}}$$

where

$r_{\beta A}$ = relatedness of β to A;
$r_{\alpha A}$ = relatedness of α to A;
$r_{\beta p}$ = relatedness of β to the population;
$r_{\alpha p}$ = relatedness of α to the population.

**Part of a thesis presented by M.S.D. to the Departamento de Genética, FMRP-USP, Ribeirão Preto, SP, Brasil, in partial fulfillment of the requirements for the Ph.D. degree. Departamento de Biologia, Universidade Federal do Maranhão, Campus Universitário do Bacanga, 65020-080 São Luís, MA, Brasil. E-mail: drummond@clo.com.br*

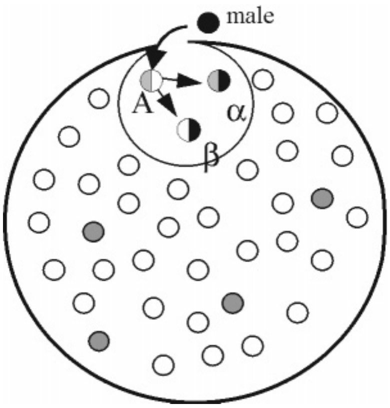

Figure 1 - Genetic relationship of individual female A with its descendents α and β. According to the genetic frequency of the neighboring population, female A has greater aggregated relatedness with α than with β. The patterns refer to the genotype of the individuals under consideration. Black = Male's allele; white = allele a^y; gray = mutant allele a^x.

What are the evolutionary implications of these considerations? According to the Hamiltonian theory, the result of an individual behaving altruistically depends on its degree of similarity to the individual being helped, that is to say, the closer the relatedness between this individual and the altruist, the more likely to occur and the more advantageous the interaction will be. However, in the evolutionary context, selection will only favor such a specific relation if it allows the altruist's gene copies to be passed on to the next generation more efficiently. Efficiency here involves both quantity and quality of the generated copies and does not depend only on the reproductive success of the altruistic individual or on that of the individual being benefited, but also on the reproductive success of all neighboring individuals in the population carrying gene copies identical to those present in the social pair under consideration. In the final analysis, efficiency depends on the altruist's gene frequency and distribution in the population.

The question of gene distribution is a little more complex and usually confused with that of relatedness. Rarer genes aggregated in a single family unit increase genetic similarity within it, whereas widespread genes determine smaller similarity. A problem, however, resides in clearly defining this basic family unit, whether a deme, a colony or an aggregation of nests. This would depend basically on two factors: a) degree of genetic isolation of the specific basic unit under consideration, and b) aggregated value of relatedness within this unit in comparison to that of the whole population. If the value of the mean aggregated relatedness of the unit under consideration is higher than the value of the mean aggregated relatedness of the whole population, a potentially basic social unit is certainly present.

Therefore, the absolute relatedness value itself is not enough. The context of such individuals must also be considered. Thus, the individual's relatedness within its particular population must be analyzed and genetic similarity level contextualized.

A key question to consider is how individuals perceive similarity in other co-specific individuals and hence decide to form family units based on characters of more aggregated value. Unlike relatedness, this is a minor problem since what matters is similarity proximity of less common key characters in the population among the individuals under consideration. This subject, well documented in the literature, reinforces the concept that recognition in social groups is phenotypic (Greenberg, 1979; Boch and Morse, 1982; Getz and Smith, 1983). However, for a newborn with no ability to discern its closest genetic relatives, such recognition must be comparative, i.e., in a given universe, among all similar individuals, some must be more similar than others. Inversely, some different individuals must be less different than others. This suggests that the capacity of an individual to evaluate aggregated relatedness value of another conspecific individual does not depend on the ability to measure genetic locus values, but rather on perception of highly hereditable secondary characteristics as a display (or signal) of social identity. The capacity to recognize such displays would make possible a given carrier's choice of the closest conspecific individuals with generally greater genetic similarity between one another in relation to the whole population. Since individuals with closer relatedness would have generally greater genetic similarity, those identifiable by such displays would also be probably more related genetically.

Together with relatedness degree, kin recognition has been considered to be central in the evolution of altruism. However, kin recognition is still a reason for questioning, among which a few shortcomings can be pointed out: a) field studies have generated inconsistent results regarding animal capacity to evaluate relatedness effectively and deciding whom and how much help should be given based on this evaluation (Bourke and Franks, 1995); b) being a social characteristic, the origin of kin recognition can be understood only in reference to a social group, leaving unanswered the question on the mechanisms that favored the formation of social groups in the first place.

In the light of these two points, particularly the second, it is clear that some other mechanism, besides kin recognition, must play a key role in social evolution. Phenotypic recognition could be that mechanism since numerous data suggest that recognition among conspecific individuals happens based on behaviors, smells, colors and shapes (Wilson, 1975; Waldman *et al.*, 1988; Bourke and Franks, 1995; Crozier and Pamilo, 1996). The central problem is determining even the possibility of distinguishing degrees of relatedness through this type of recognition.

The aggregated relatedness model proposed in this work does not affect in any way the theoretical assumptions of kin selection. On the contrary, in addition to further clarifying the kin selection mechanism, it also introduces a new view of the problem at the structural level of population genetics, allowing comprehension of some apparently conflictive phenomena, particularly in the species not highly socially structured or presenting relatively low degree of relatedness.

ACKNOWLEDGMENTS

I thank Professors Warwick Estevam Kerr, David de Jong, Lucio Antonio de Oliveira Campos, Gabriel Augusto Rodrigues de Melo, Lenira de Melo Lacerda and Juvenal Cordeiro Silva Junior for reading the manuscript and for their suggestions. I am grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support.

RESUMO

Dados de campo de espécies de Hymenoptera primitivamente sociais têm se mostrado contraditórios quanto ao papel do reconhecimento de parentes e do grau de parentesco na evolução social. Nesse trabalho um novo conceito de “coeficiente de parentesco” foi desenvolvido. Esta nova hipótese foi chamada de “parentesco agregado”. Nesse conceito, genes compartilhados por dois indivíduos quaisquer têm importância significativa na formação das unidades familiares, dependendo de suas freqüências e da forma como estão distribuídos na população circunvizinha a esta unidade familiar.

REFERENCE

Boch, R. and **Morse, R.A.** (1982). Genetic factor in queen recognition odors of honey bees. *Ann. Entomol. Soc. Am. 75*: 654-656.

Bourke, A.F.G. and **Franks, N.R.** (1995). Social evolution in ants. In: *Monographs in Behavior and Ecology* (Krebs, J.R. and Clutton-Brock, T., eds.). Academic Press, Princeton, pp. 529.

Crozier, R.H. and **Pamilo, P.** (1996). Evolution of social insect colonies: Sex allocation and kin selection. In: *Oxford Series in Ecology and Evolution* (May, R. and Harvey, P.H., eds.). Oxford University Press, New York, pp. 306.

Getz, W.M. and **Smith, K.B.** (1983). Genetic kin recognition: honey bees discriminate between full and half sisters. *Nature 302*: 147-148.

Greenberg, L. (1979). Genetic component of bee odor in kin recognition. *Science 206*: 1095-1097.

Hamilton, W.D. (1964). The genetical evolution of social behaviour, I and II. *J. Theor. Biol. 7*: 1-52.

Waldman, B., Frumhoff, P.C. and **Sherman, P.W.** (1988). Problems of kin recognition. *Trends Ecol. Evol. 3*: 8-13.

Wilson, E. (1975). *Sociobiology: the New Synthesis*. Harvard University Press, Cambridge, pp. 697.

(Received March 23, 1999)