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Source: *Evolution*, Vol. 37, No. 2 (Mar., 1983), pp. 417-420

Published by: Society for the Study of Evolution

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Evolution, 37(2), 1983, pp. 417-420

PROBLEMS IN THE USE OF GENETIC SIMILARITY
TO SHOW RELATEDNESS

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Received March 24, 1981. Revised May 24, 1982

Genetic heterogeneity from allozyme data in social mammals has received recent attention as a tool to show degree of relatedness among colony members. Whether one is considering a colonial anemone, a prairie bunchgrass, or a swarm of insects, the idea of using electrophoretic genetic heterogeneity as a tool to infer relatedness in social organisms is appealing. In many instances a naturally occurring aggregation may be readily observed, but relatedness among group members is known only by observing a population until a complete turnover of individuals occurs. For many long-lived species, or species with complex or obscure life cycles, this is impractical. Here we used data we have obtained from a social mammal to evaluate the use of electrophoretic genetic heterogeneity to determine relatedness.

If social groups are kin groups, sociality may result from behaviors which favor the incorporation of known individuals, who are likely to be closely related, into the society and the rejection of strangers, who are likely to be unrelated or distantly related. Thus, sociality may result from kin selection and inclusive fitness (Hamilton, 1964; West Eberhard, 1975). Qualitative conditions that promote genetic heterogeneity among social groups and increase the relatedness of group members include: (1) the restriction of mate selection to those within the social group, (2) a low exchange rate of individuals among groups, and (3) preferential recruitment of juveniles into their natal group (McCracken and Bradbury, 1978). These criteria were used by McCracken and Bradbury in evaluating the kinship within colonies of phyllostomid bats on the island of Trinidad. They found that all juveniles dispersed from their natal colony, that recruitment into harems was random, and that harems and colonies were not heterogeneous at three allozyme loci. Thus they concluded that relatedness among colony members was low and sociality in this species at this location was not a result of kin selection. Here we consider the opposite case in which

genetic heterogeneity among social colonies is present and relatedness within these colonies is known to be high.

The population biology and behavior of the yellow-bellied marmot (*Marmota flaviventris*), a large, social, ground squirrel inhabiting the mountainous regions of western North America, is the subject of a 20-year continuing study by the junior author in the East River Valley of Gunnison County, Colorado. In the East River Valley marmots occur where large boulders are associated with nearby meadows. Such habitat is patchy, occurs in a continuum of patch sizes, and in larger patches social, polygynous colonies are found. The typical polygynous group consists of a territorial male, a harem of two or three females, yearlings, and young of the year (Downhower and Armitage, 1971).

We reported the structure of the East River Valley marmot populations relative to the conditions defined by McCracken and Bradbury (Schwartz and Armitage, 1980): (1) Mate selection was restricted to residents of each colony. The allozyme phenotypes of 66 young from 26 litters supported the hypothesis that the young were produced by colony residents without exception. (2) Intercolony movements were limited. Only 40 of 790 marmots studied between 1962 and 1977 moved from one of our study sites to another; only 15 of those moves resulted in gene flow as indicated by subsequent reproductive activity. (3) Only females were preferentially recruited into their natal colony. The rate of intracolony female recruitment from those colonies with stable social structure averaged 0.61. Ninety-five percent of males were recruited from outside the natal colony and outside our study sites and thus were of unknown origin. Significant electrophoretic heterogeneity in eight allozyme loci occurred in nine colonies.

With these data we evaluate the utility of using allozyme data to infer relatedness.

MATERIALS AND METHODS

Each summer since 1962, marmots were trapped, ear tagged, marked with a black fur dye for individual recognition, social relations within colonies were observed in excess of 250 hours, and relatedness of

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all colony residents was determined (Armitage, 1974, 1975). Blood was sampled during the summers of 1976 and 1977 from the femoral vein of all members of nine colonies that contained 41 male and 34 female young or yearlings and 17 male and 20 female adult (2 years or older) resident marmots. Eight variable allozymes with two alleles at each locus were identified using standard techniques of starch gel electrophoresis (Selander et al., 1971).

RESULTS AND DISCUSSION

Inferring relatedness through genetic heterogeneity is an argument contingent on the magnitude of the observed heterogeneity. This magnitude is a complex function of the degree of inbreeding, deme size, selection, assortative mating, rate of gene flow, and differential fertility. The difficulty or impossibility of measuring many of these factors in nature prevents the use of the magnitude of heterogeneity as a simple tool. An additional problem is that alleles that are identical by direct descent from a close relative cannot be distinguished from those identical in nature (i.e., identical in state or kind). However, we hypothesize that related individuals should have a higher average electrophoretic genetic similarity than unrelated individuals.

Allozyme systems identified and the average frequencies of the most common allele in the nine marmot colonies were: Esterase-2 (*Es-2*) 0.61; Esterase-1 (*Es-1*) 0.77; Transferrin (*Tf*) 0.89; Phosphoglucosomutase (*Pgm*) 0.92; Leucine aminopeptidase (*Lap*) 0.97; Phosphoglucosomerase (*Pgi*) 0.99; Esterase-3 (*Es-3*) 0.99; and Esterase-4 (*Es-4*) 0.99 (Schwartz and Armitage, 1981).

We calculated a genetic similarity index for each pair of individuals in each colony which was equivalent to Roger's index (*S*) (Rogers, 1972).

$$S = 1 - \left(\frac{1}{2} \sum_{i=1}^m (P_{i,x} - P_{i,y})^2 \right)^{\frac{1}{2}}$$

where $P_{i,x}$ is the frequency of the $i + n$ allele in individual x and m is the number of alleles ($m = 2$). In a diploid organism there are a maximum of two alleles possible in each individual, therefore the frequency of an allele was 1.0, 0.5 or 0.0, and individuals with identical genotypes have an index value of 1.0, heterozygotes paired with a homozygote have a value of 0.5, and homozygotes with different alleles a value of 0.0. We also calculated genetic similarity using Nei's index (Nei, 1972) but this index produced poorer correlations between relatedness and genetic similarity (a homozygote paired with a heterozygote had a similarity of 0.7071) than those reported below. We then calculated coefficients of relationship (r) using path analysis on pedigrees (Falconer, 1960) for each pair (all combinations of colony members taken two at a time) of individuals within each colony in 1976 and 1977. The pedigrees from our study sites extend back to 1962. Untagged immigrants were assumed to be unrelated to any colony resident.

The use of a genetic similarity index in ascertaining relatedness has obvious weakness. Siblings produced by parents that were both heterozygous could

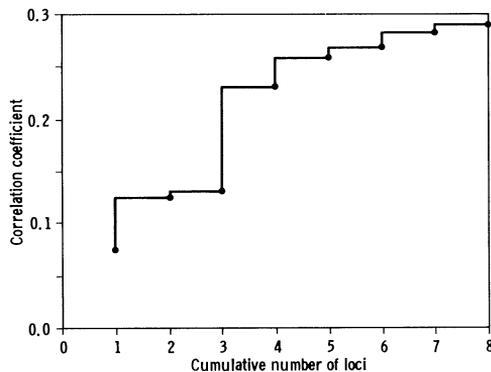


FIG. 1. The correlation coefficient of genetic similarity and relatedness (calculated by path coefficients) plotted against the cumulative average of one to eight loci. The loci were averaged in order of increasing frequency of the most common allele.

have a genetic similarity of 0.0 for a locus, but their relatedness in alleles would average 0.5. An allele with a frequency near 0.5 in the total population could be present in an unrelated immigrant in the colony. If that allele were present in high frequency among related colony members, the immigrant and colony members would have a high genetic similarity index and would appear to be closely related. Also, little information would be provided by alleles with a frequency of 1.0 in most colonies; however, bearers of a rare allele within a colony probably are closely related. We therefore questioned what allelic frequencies would be most useful in ascertaining relatedness from genetic similarity.

To determine the strength of the relationship between genetic similarity and relatedness for pairs of individuals (relative to allele frequency) we calculated correlation coefficients between genetic similarity and relatedness for each locus: *Es-2* (0.073); *Es-1* (0.105); *Tf* (0.032); *Pgm* (0.263); *Lap* (0.132); *Pgi* (0.079); *Es-3* (0.115); and *Es-4* (0.118). The lowest correlation coefficient was that of *Tf* and the highest was that of *Pgm*, but their allelic frequencies at 0.89 and 0.92, respectively, were similar and intermediate to common and rare alleles at other loci. Hence, there was no simple relationship between allelic frequencies and the correlation coefficient. The high correlation coefficient of *Pgm* was due to the birth of three large litters bearing the less common allele. The less common allele was largely associated with parents and siblings in two colonies and is an example of the mechanism that generates heterogeneity among colonies. Transferrin alleles were more evenly distributed among the nine colonies. Thus, the history of an allele in a population may confound any association between genetic similarity and relatedness.

The linear correlation coefficient between relatedness and the cumulative average of genetic similarities increased monotonically as each additional locus was included in the average (Fig. 1). Therefore,

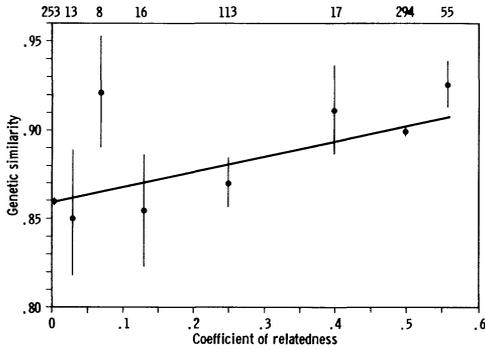


FIG. 2. The relationship of genetic similarity (average of eight loci) to the coefficient of relatedness between pairs of colony members. The regression equation is significant ($Y = 0.086X + 0.86$, $F_{1,767} = 69.1$, $P < .001$). The numbers at the top of the figure are the sample sizes of pairs of marmots with the same degree of relatedness. Vertical lines are 95% confidence interval around the mean of genetic similarity of those marmots with the same degree of relatedness.

the best predictor of relatedness is based on the maximum number of variable loci.

Although average genetic similarity was positively related to the coefficient of relationship (Fig. 2), the predictability of relatedness from genetic similarity was low ($r^2 = 0.083$). Hence with our data, errors inherent in a genetic similarity index preclude its usefulness to predict relatedness.

We then tested the relationship between the average relatedness of colony members and their genetic similarity (Fig. 3). The low predictability ($r^2 = 0.003$) of average colony relatedness from genetic similarity for our data suggests that the distribution of allozyme variability among social groups has no utility to quantitatively predict relatedness in studies of social evolution. Allozyme and demographic data as used by McCracken and Bradbury (1978) seem valid in showing qualitatively the absence of relatedness or distant relatedness. A quantitative prediction of relatedness perhaps may be found in organisms where there are more variable loci, more alleles at loci than in our data, or when both conditions occur.

We next pursued a qualitative analysis. The mean and 95% confidence intervals of genetic similarity among most colonies with average relatedness of 0.3 or greater did not overlap the mean of the genetic similarities of 253 pairs of unrelated marmots (shown by the arrow in Fig. 3). This pattern suggests high relatedness among colony members. A comparison of genetic similarity values in colonies with the similarity values of randomly chosen intercolony pairs would generate this distribution in many situations. As an example, the average genetic similarities of four marmot colonies located in North Pole Basin

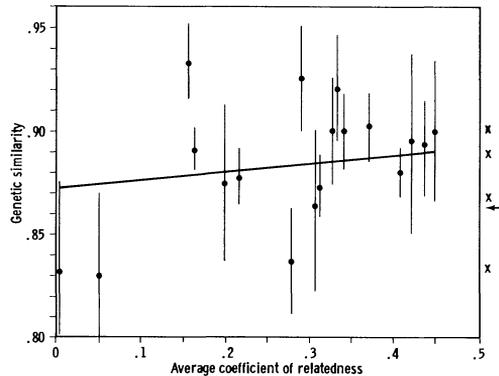


FIG. 3. The relationship of genetic similarity (average of eight loci) between colony members and the average relatedness among colony members. The regression is non-significant ($Y = 0.038X + 0.87$, $F_{1,767} = 2.5$, $P = .14$). Vertical lines are the 95% confidence interval around the mean genetic similarity of each colony calculated for colony members in 1976 and 1977. The arrow points to the mean genetic similarity of 253 pairs of marmots known to be unrelated. The "X" symbols are the mean genetic similarities of four North Pole Basin colonies in which the relatedness of pairs of colony members is not completely known.

(NPB), Gunnison County, Colorado, were plotted (X symbols) on the right of Figure 3. This site was studied for five years and the social structure was similar to that in the East River Valley (Johns and Armitage, 1979). However, the relatedness of some colony members is still unknown. The high average genetic similarity among members of three colonies suggests relatedness comparable to that of colonies in the East River Valley.

Social substructure and population characteristics of marmots create genetic heterogeneity. Relatedness is high among colony members. There is no quantitative predictability between relatedness and allozyme similarity within colonies as shown by our data. Electrophoretic data have a qualitative utility in detecting mate selection outside the social system (McCracken and Bradbury, 1978) or in showing multiple insemination (Metcalf and Whitt, 1977). Genetic homogeneity coupled with easily observed demographic processes may reveal a lack of relatedness among colony members (McCracken and Bradbury, 1978). Our data suggest that high genetic similarity, when compared with the genetic similarity of animals known not to be descendant or collateral kin, qualitatively implies relatedness among social group members.

The detection of relatedness in the social structure of populations is essential in order to understand how individual reproductive strategies are expressed in social dynamics and population regulation. Kin and non-kin are not treated alike (Johns and Armitage,

1979) and the spatial patterning of many mammalian species may consist of nearest-neighbor kin-groups (e.g., Armitage, 1973; Dunford, 1977; Michener, 1979; Madison, 1980). Therefore, understanding the role of social dynamics in population regulation and the evolutionary basis of this role requires knowing the relatedness of individuals in the population.

SUMMARY

Seventeen years of observation and trapping in nine marmot colonies have allowed the calculation of the coefficient of relatedness (r) for each pair of colony members using path analysis. Relatedness among colony members could not be predicted quantitatively from the regression between average colony relatedness and genetic similarity expressed at eight allozyme loci. The mean and 95% confidence interval of genetic similarity in those colonies where relatedness was high frequently did not overlap the mean genetic similarity of pairs of marmots known to be unrelated. This pattern may be used to infer high relatedness among colony members.

ACKNOWLEDGMENTS

We thank J. Amos, C. Baker, J. Endler, M. S. Gaines, J. Hamrick, P. Hedrick, R. S. Hoffmann, and G. McCracken for their advice, encouragement, and for critically reading drafts of this manuscript. This study was supported by National Science Foundation grant BMS 74-21193 and University of Kansas Biomedical grant 4442 to K. B. Armitage.

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