

Isolation by Distance in Bougainville

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ABSTRACT The technique of population structure analysis based upon the model of Malécot is applied to blood polymorph, anthropometric, and demographic data collected from residents of south-central Bougainville Island, Territory of New Guinea. The results from these several analyses are relatively consistent and support the idea that this theoretical model can be applied successfully to real sets of biological data and that useful conclusions can be reached concerning the breeding structure of human populations. A comparison of population structures from various parts of the world reveals how fragmented the breeding structure in Melanesia is, and how relatively rapidly the coefficient of kinship declines over distance in that area.

According to the theoretical model of Malécot (1) the mean coefficient of kinship, ϕ , between two randomly chosen individuals declines with the distance, d , between their places of birth as follows:

$$\phi(d) = ae^{-bd}$$

where the parameters a and b are related to local inbreeding and systematic pressures, respectively. Morton *et al.* (2) have developed promising techniques of bioassay, utilizing blood polymorphs, anthropometric measurements, and demographic information, which provide for the application of this model to actual populations. However, it is one matter to fit an exponential curve to estimated values of ϕ ; it is quite another matter to have much confidence in a strict interpretation of the values of a and b that obtain. It is only through the comparison of estimates of ϕ , a , and b from different genetic and biological variables from the same population that their reliability and consistency can be determined.

Blood polymorph, anthropometric, and migrational data collected from residents of a small region in south-central Bougainville Island (Territory of New Guinea) during 1966-67 provide an opportunity for such comparisons (Fig. 1). The reported patterns of extreme blood polymorph and anthropometric variation in this area are roughly comparable and seem to reflect the known linguistic, demographic, and historical relationships of the different groups in this area (3). They imply that (a) the breeding structure of the population is highly fragmented and the major boundaries to gene flow are connected to linguistic differences and to geographic distance; (b) this breeding structure has enabled an accumulation of inbreeding effects over time, primarily due to population subdivision rather than to preferential consanguineous marriage; and (c) such effects seem to be reflected not only in the blood polymorph allele frequencies but in anthropometric differences as well.

It is with the quantitation of these implications that this paper is concerned. The principal problems are (a) how much of an inbreeding effect is recognizable from the blood polymorph and demographic data, (b) do different sorts of biological data give significantly different estimates for ϕ , a , and b , and (c) how do these compare with results from other parts of the world.

The polymorph systems in these 19 villages were analyzed by the techniques developed at the Population Genetics Laboratory of the University of Hawaii and embodied in the ALLTYPE and DISTAN computer programs (4).^{*} These programs generate estimates, y , of ϕ for each of the 10 distance classes used in the analysis, and then fit Malécot's function to these observed estimates. These values for each system, and the best curve fitted to them, are given in Fig. 2 (5). The chi square (χ^2) test for heterogeneity for a and b over all systems gives a value of 25.013 with 19 degrees of freedom, so that there is no evidence of systematic pressures acting on the different systems in this small area, and the different estimates cannot be rejected as being heterogeneous. Also, the overall estimates of a and b are extremely high, $a = 0.051$, $b = 0.105$.

Fig. 3 compares these values with previous results of population-structure analyses of selected groups of Micronesians, New Guineans, and more technologically advanced groups (nordestino Brazilians, Swiss mountaineers, and Japanese). The values of a for the technologically primitive groups clearly form a class distinct from the more advanced populations, differing from them by about a factor of 10. The rate of decline of ϕ over distance, described by b , is extremely high for Bougainville and New Guinea, but is quite low for Micronesians, reflecting the dispersal over a large area of a small, highly interrelated population. Corrections for population density would align the Micronesian values more closely with the New Guinea and Bougainville values. It is from such a comparison that the relatively monolithic nature of the Bougainville blood polymorph results becomes more convincing.

Within Bougainville, the high estimates of a and b are attributable to extreme population subdivision. This would lead both to increased localized inbreeding (high values of a) and to small standard deviations in marriage distances (resulting in high values of b).

Estimates of ϕ , a , and b for a population can also be derived from information on the incidences of marriages of individuals separated at birth by different distances. The program NUMIX will accept a matrix of migration probabilities between groups and, starting with assumed panmixia, will compute the accumulation of kinship for succeeding generations

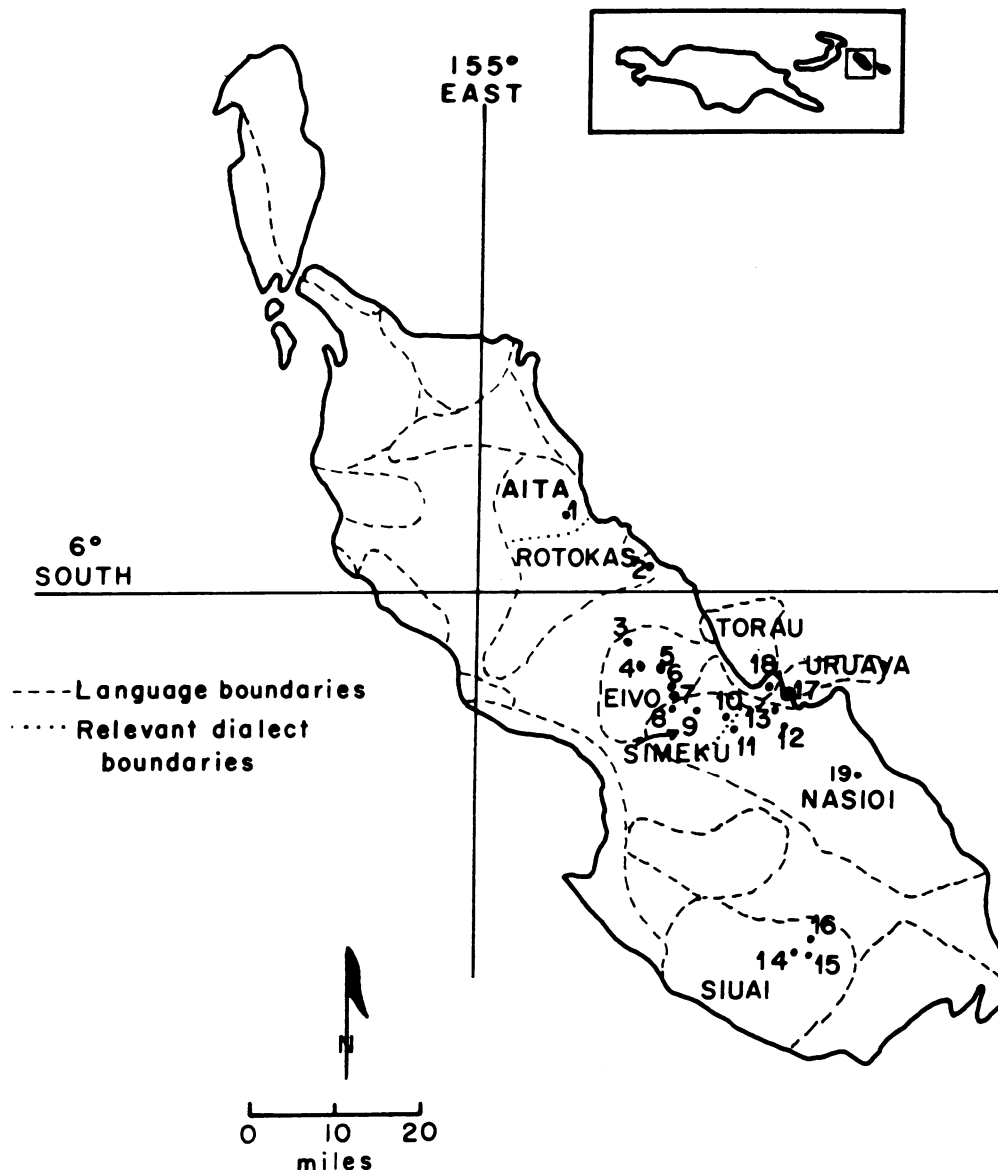


FIG. 1. Bougainville Island, Territory of New Guinea. Numbers refer to villages sampled (3).

until equilibrium is reached, under the assumptions that the migration probabilities and the sample size remain constant (6). The resulting table of estimates of ϕ was analyzed by the DISTAN program; the curve fitted to these estimates has values of $a = 0.0588$, and $b = 0.0954$, in excellent agreement with the overall curve for the blood polymorphs.

By means of a number of additional assumptions, anthropometric measurements may also be used to furnish estimates of ϕ , a , and b . In an attempt to calculate some upper estimates for these parameters, I used, instead of single measurements on individuals, the scores of individuals on the major discriminant function that maximally separates these villages (3). For the fitted curve, $a = 0.054$ and $b = 0.232$, but all estimates have a large standard error.

The analysis of pedigrees in nonliterate societies is filled with hazards but it has been attempted in one small area of the sample, where Oliver (7) had recorded genealogies in 1938-39. Even so, the pedigrees I have been able to re-

construct for the current generation are quite short, being incomplete for many individuals for relationships more distant than first cousins. These were analyzed using the program COEF (8), which performs the calculation

$$F = \sum_A 2^{-n_1 - n_2 + 1}$$

where n_1 and n_2 are the number of generations between the common ancestor and the propositus through the father's line and the mother's line, respectively, and the summation is over all common ancestors. The resulting inbreeding coefficient is 0.008 for the current generation, within an area of radius 4.5 kilometers, as compared to the value of the coefficient of kinship for the 5-km class of 0.03403. This indicates that, unlike the Brazilian situation, for example, the accumulated amount of inbreeding evident in the population cannot be recovered by the analysis of short pedigrees.

In conclusion, this study represents a successful applica-

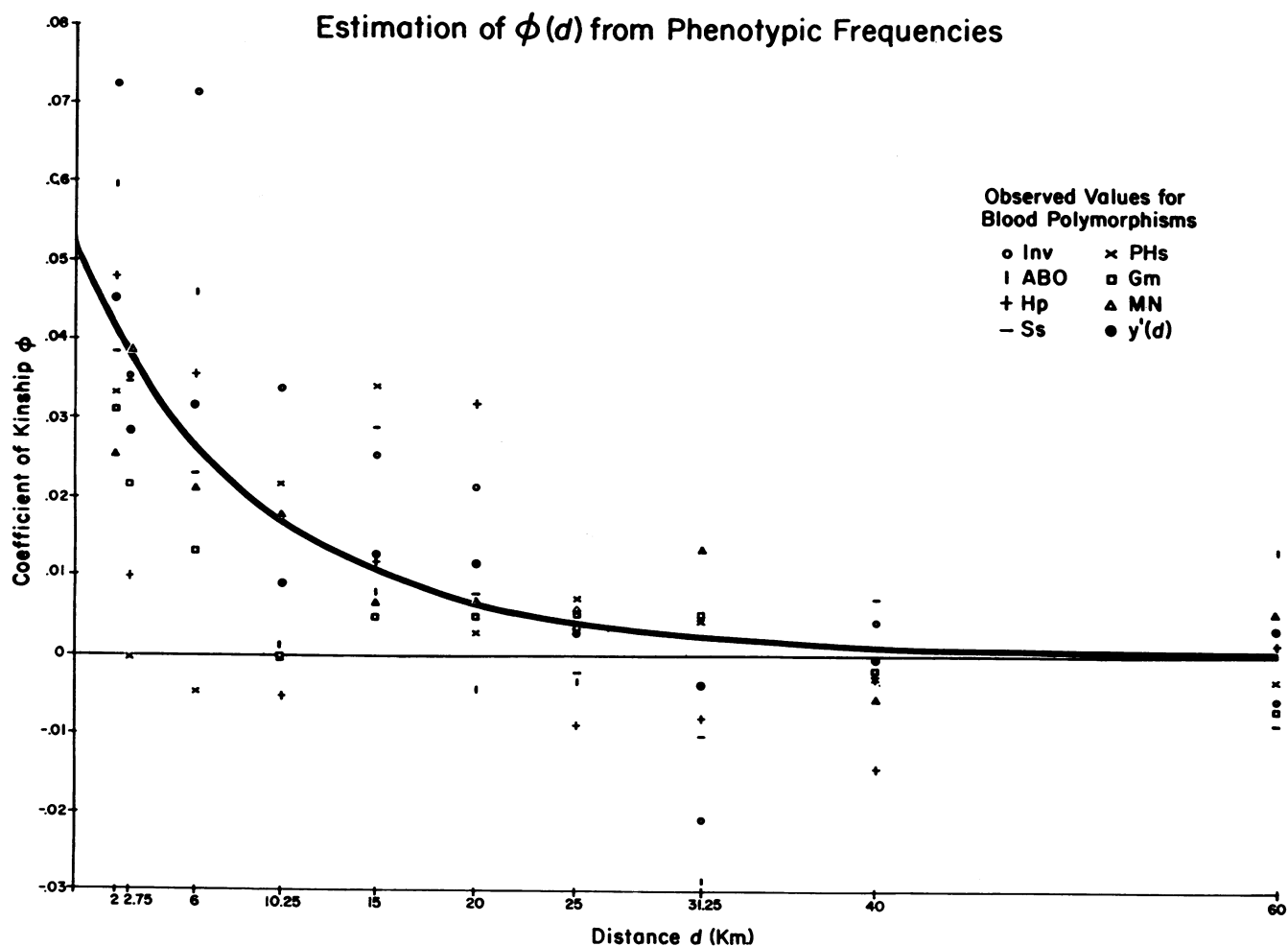


FIG. 2. Values obtained for individual systems, and their standard errors of estimate, are given elsewhere (5).

tion of the techniques of population structure analysis to a set of real biological data. The attention to short-range relationships in this sample, and also the likelihood that the structure of the Bougainville population has been relatively constant for at least the last 2000 years, are the most likely reasons for the homogeneity of estimates of a and b .

In comparing my results with those of previous studies, a consistent dichotomy is apparent when mobile, populous, and technologically advanced groups are contrasted with the more fragmented and inbred structures of the gardeners of the tropics. It will be surprising if the values of both a and b for the Melanesian populations of Bougainville and New Guinea are exceeded in future studies. Traditionally, these people were tied closely to their garden plots and had no strong political alliances beyond their immediate neighborhoods, a situation conducive to extreme population subdivision. Although the population structure of hunter-gatherers has not yet been reported, it is likely that these more mobile groups are less isolated over distance than the Melanesians. It may well be that the most extremely fragmented population structures in the history of *Homo* are those characteristic of neolithic gardeners.

*** NOTE ADDED IN PROOF**

Henry Harpending of this department has found that the estimates of ϕ calculated by DISTAN include not only ran-

dom kinship, but also localized inbreeding. This means that the values of b reported here could be estimated more accurately, but the conclusions concerning the relative homogeneity of estimates within Bougainville and the comparisons with other populations stand.

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Coefficients of Kinship for Selected World Populations

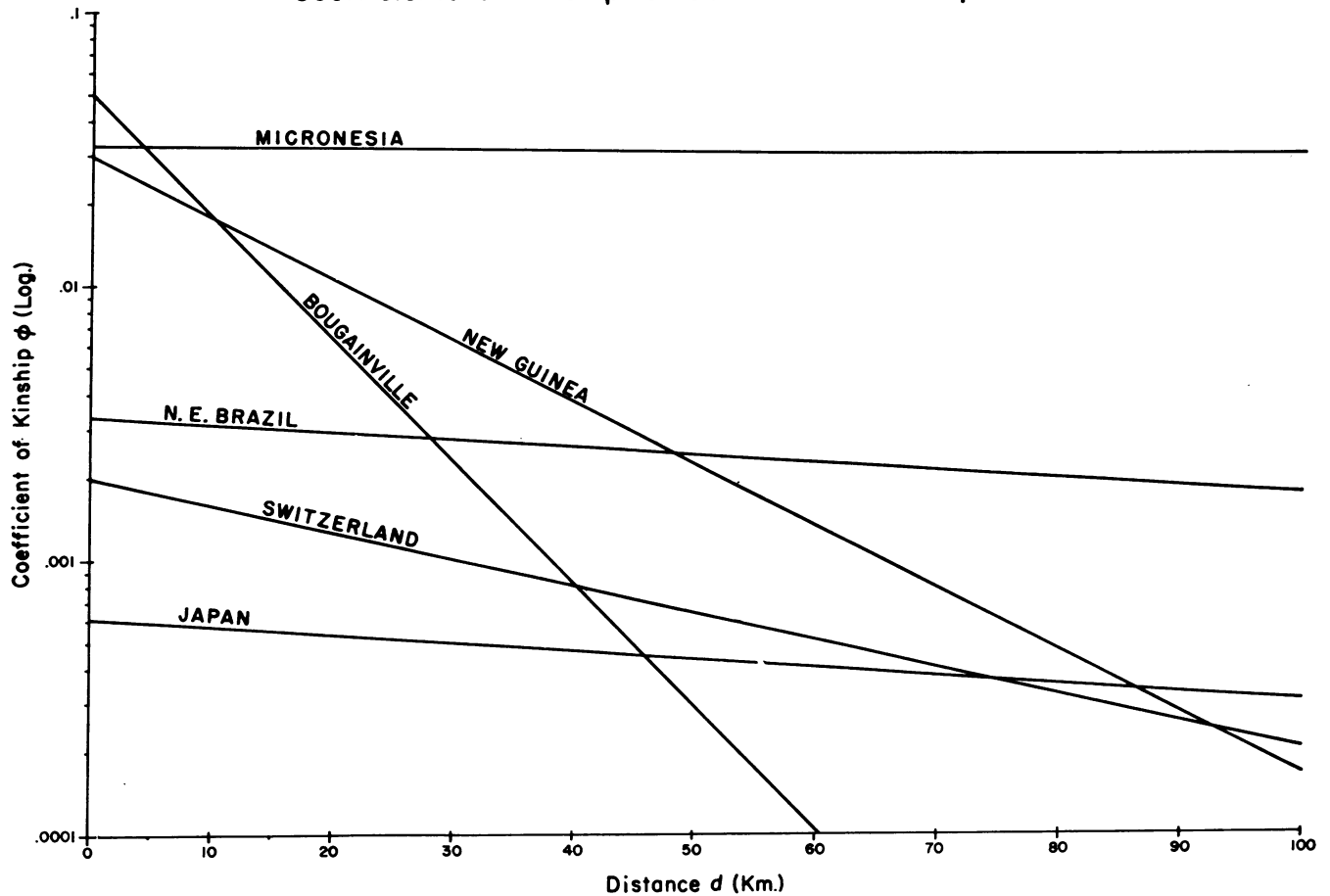


FIG. 3. Comparative data are taken from Imaizumi and Morton (9).

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