Gene Frequencies and Microdifferentiation among the Makiritare Indians. IV. A Comparison of a Genetic Network with Ethnohistory and Migration Matrices; a New Index of Genetic Isolation

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The preceding three papers in this series have characterized seven different villages of the Makiritare Indians of southern Venezuela with respect to 27 different genetic systems. The present paper will summarize the amount and nature of the genetic microdifferentiation between villages revealed by these data. We will then present the recent history of the tribe, and compare the biological relationship between villages suggested by this history with the relationship suggested by the phylogenetic approach of Cavalli-Sforza and Edwards (1967), utilizing in this approach the above-mentioned genetic systems. The migration matrices of the inhabitants of the several villages concerned will be presented and the rather striking fashion in which the dynamics of these villages differ from those of the villages of agricultural-type populations discussed. Some of the implications of these differences will be explored. An index of genetic isolation will be developed, intended to supplement treatments of isolation by geographic distance.

GENETIC MICRODIFFERENTIATION

As reported in the appropriate papers in this series, the frequency of individual genes at such variable loci as the Rh, MNSs, haptoglobin, and phosphoglucomutase systems varies greatly from one village to the next; that is, there is by inspection marked genetic microdifferentiation. As we have pointed out in the past (Neel 1967; Gershowitz et al. 1967), in our opinion the usual statistical tests of the significance of these differences cannot be utilized, because of the relatively high coefficient of relationship between the individuals comprising a village and because the majority of the members of each village have been studied, making this more of an enumerative than a sampling procedure. Recently Smith (1969) has shown how misleading the usual χ^2-type levels of significance can be under these circumstances, and has suggested approximate alternatives. Although this constitutes an important step forward, the necessary assumptions underlying his approach are often not realized in Indian villages and we shall still refrain from simple statistical comparisons between villages.

One way to quantitate the degree of microdifferentiation is by using genetic dis-

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tance functions, although assigning variances to them is complicated by the same factors that raise difficulties in using χ^2. The issues raised by the use of these functions are theoretical (e.g., the merits of the various functions) and pragmatic (e.g., the comparison of results employing different data sets). In the present treatment we will employ the distance function of Edwards and Cavalli-Sforza (1964), reserving for later a comparison of these results with such other approaches as the modified function of Cavalli-Sforza et al. (1969) or that of Balakrishnan and Sanghvi (1968), and a discussion of certain theoretical issues. On the more pragmatic side, the large number of polymorphisms investigated in this study provides an opportunity for a simple comparison of the results of employing differing sets of loci. In our previous reports on genetic distance between Indian villages and tribes (Fitch and Neel 1969; Neel and Ward 1970), the function was based on the Rh, MNSs, Kidd, Duffy, Diego, and

TABLE 1

COMPARISON OF GENETIC DISTANCES DERIVED FROM TWO INDEPENDENT SETS OF LOCI

	Village						
	A	BD	C	E	F	G	HI
Village:							
A	.....	.362	.558	.353	.345	.268	.336
BD	.206	.....	.250	.221	.432	.314	.296
C	.400	.218	.....	.393	.588	.485	.444
E	.249	.094	.197	.....	.379	.249	.273
F	.332	.221	.338	.262	.....	.394	.383
G	.301	.177	.268	.137	.307	.....	.158
HI	.350	.158	.141	.134	.296	.182	.....

NOTE.—Upper triangular matrix (six loci)—Rh, MNSs, Duffy, Kidd, Diego, and haptoglobin; lower triangular matrix (five loci)—P, Lewis secretor, Gc, acid phosphatase, phosphoglucomutase.

haptoglobin loci (16 alleles), simply because these were the six polymorphic loci for which a large number of tribes had been studied. Of the 27 genetic loci investigated in the present study, there are five others characterized by genetic polymorphisms where the frequencies of the constituent genes are in the range of the six above-mentioned systems. These are the P, Lewis secretor, Gc, acid phosphatase, and PGM_1 loci (10 alleles). The Lp locus also exhibits considerable variation in the frequency of the Lp(a+) allele, but for reasons discussed in Arends et al. (1970) is not yet felt to be sufficiently well understood for these purposes. Table 1 presents the pair-wise genetic distances between the seven Makiritare villages of this study based on these five systems, compared with the previous results based on six different systems. The six-system results are, incidentally, quite comparable in magnitude to those encountered earlier in a similar study of Yanomama Indian villages (Neel and Ward 1970).

In this approach, for each locus, the set of populations is initially conceived as being embedded on the surface of a unit hypersphere (radius equals one) of finite dimensions (equal to the number of alleles) with coordinates based on the direction cosines resulting from the gene frequencies. The distance between pairs of populations is measured on the surface of the hypersphere, and then projected into Euclidean space. We have followed Cavalli-Sforza and Edwards (1967) in using the chord as a

first approximation to such a projection. The overall pair-wise value, D, represents a distance in Euclidean space of finite dimensions (equal to the number of loci), obtained by summing the contributions of each locus projected onto the hyperplane, by the theorem of Pythagoras. Algebraically, for a single locus with m alleles, two populations are given the chord distance $d = (2\sqrt{2}/\pi)\sqrt{1 - \cos\theta}$, where

$$\cos\theta = \sum_{i=1}^{m}\sqrt{p_i q_i}$$

and p_i, q_i are the frequencies in the respective populations of the ith allele. The total distance, D, is obtained from the distances resulting for each of the n loci by squaring each and extracting the square root of the sum, that is,

$$D = \sqrt{\sum_{j=1}^{n} d_j^2}\,.$$

Because a different number of systems has been employed in the calculation of the two sets of distances, and because two of the systems in the one calculation are characterized by multiple alleles, a direct comparison of the findings has no significance. In theory, the distance function could be expressed in terms of mean distance per locus or per allele, thus permitting a direct comparison, but since we have selected these loci just because they are variable, such a comparison would have very limited use. However, we can ask whether the relative distances between villages remain the same in the two matrices. Should these differ widely, then the phylogenetic schema (or genetic network) connecting the villages will also vary. Cavalli-Sforza et al. (1969) have approached this question by using a standard coefficient of correlation. Because of doubts concerning the normality of the distance distribution, we propose to employ instead Spearman's nonparametric rank correlation coefficient. Thus, assigning ranks to the pair-wise genetic distances between villages as determined by the Rh-MNSs-Kidd-Duffy-Diego-haptoglobin loci and by the P-Lewis secretor-GC-AP-PGM_1 loci, we calculate the coefficient as $r_s = 1 - 6(\Sigma d_i^2)/N(N^2 - 1)$ where d_i is the difference in ranking between the two sets of distances for the ith pair-wise distance. We find $r_s = .529$. This value is significant at the 1% level (Kendall 1962) but the extent of the departure from a perfect correlation is noteworthy. Inspection of table 1 reveals some marked discrepancies between the relative magnitudes of the pair-wise distances (e.g., the distance between villages C [Wasaña] and HI [Acanaña] is ranked fourth on the basis of the set of six loci but is ranked eighteenth on the basis of the independent set of five loci). The comparison has the defect that in one case 16 and in the other case 10 alleles are involved; the discovery of additional polymorphisms will permit better comparisons. Furthermore, two of the systems in the five-system distance function (AP, PGM_1) are characterized by low frequencies of the second allele. Not only is there a possible problem with "boundary effects," but in small finite populations of this type, because of the biological interrelations of the individual comprising the sample, uncommon genes occur in family clusters; that is, if one encounters one individual with the trait, he may expect to encounter several more. The degree to which these effects bias the distance function is not yet clear.

The significance attached to the observed difference between the two sets of dis-

tances depends on the magnitude of the sampling error associated with the distance function. Cavalli-Sforza et al. (1969) have evaluated the significance of pair-wise genetic distances by presenting a standard error based on the variation between loci in their contribution to the distance function. While this approach is valid in the case where the distribution of the distance functions for each locus can be considered identical, we do not feel justified in assuming that this situation pertains in the population we are studying. The expected mean distance will only be the same for all loci when each locus is constrained in the same way by the same set of deterministic factors (selection, migration, etc.), an inherently unlikely situation. Therefore, we have elected to treat the contribution of each locus to the distance function as if it were unique.

Three caveats may be entered against basing a rank correlation coefficient on distance data of this type; the same objections appear to apply with equal or even greater strength to a standard correlation:

1. In the triangular matrix of order $K - 1$, which sets out the pair-wise distance functions for K populations, only $K - 1$ of the $K(K - 1)/2$ elements are fully independent; that is, for any population there is a vector of $K - 1$ independent pair-wise distances, but once this vector is specified, the values that the elements can take on in each successive vector (of order $K - 2$, $K - 3$, etc.) become progressively more restricted.

2. The component, presumably unlinked, loci that make up the two sets of distance functions are not independent, but are related due to the joint effects of migration, selection, and drift acting on the population. This correlation will be incorporated in the distance function summed over all loci and will lead to correlation among the distances both between and within different matrices.

3. Since the distance functions we are using (i.e., chords) are merely functions of the differences between allelic frequencies at a locus, the correlations existing between alleles at a locus will also be incorporated into any calculated correlation.

It is not entirely clear to what extent these points affect the use of rank correlations in this context and so weaken the preceding conclusions. At any rate, it seemed likely that the most stable distance function would be based on all 11 loci; this set of distances is given in table 2. In a later section we will return to the three genetic networks which can be derived from these three sets of distances.

The mean pair-wise genetic distance between these seven Makiritare villages, utilizing the six-gene approach, is 0.356 units. The mean pair-wise distance between 12 Indian tribes of Central and South America, on the basis of the same six loci, was 0.385 units (Neel and Ward 1970). Cavalli-Sforza and Edwards (1964) utilized data on gene frequencies at five loci from 15 different widely separated ethnic groups in their treatment of genetic phylogenies. Dr. Anthony Edwards has kindly sent us the original data. Utilizing our same program, the mean distance between these groups is 0.656. The distances are not strictly comparable, since their data utilize the ABO, MNSs, Rh, Duffy, and Diego loci (19 alleles), whereas our treatment, as earlier noted, is based on the MNSs, Rh, Duffy, Diego, haptoglobin, and Kidd loci (16 alleles). We note, however, that not only is the intratribal variation almost as great as the intertribal, but, to a first approximation, the village distances are almost half as large as the distances between major ethnic groups.

RECENT HISTORY OF THE MAKIRITARE

One factor in the origin of these rather striking genetic differences between Indian villages is to be found in the traditional settlement patterns of Indian tribes (see Neel and Salzano 1964, 1967). Data collected in the course of our field work with the Makiritare provide an opportunity to compare the stated origins and relationships of the various villages with a derived migration matrix and with the genetic network uniting villages. While our primary concern in this section is to describe the historical events relevant to the seven villages we have studied and discuss the implications of these events for the maintenance of genetic variability between villages, this cannot be done without reference to what little history is known for the Makiritare tribe. Our chief sources of information have been informants in the several villages, for despite the relative cultural advancement of the Makiritare, they remain little studied. However, we have found the following works useful: Koch-Grünberg (1917),

TABLE 2

DISTANCE MATRIX FOR SEVEN MAKIRITARE VILLAGES (11 LOCI)

	VILLAGE					
	BD	C	E	F	G	HI
Village:						
A	.417	.687	.432	.479	.403	.485
BD	.....	.332	.240	.486	.360	.335
C	.....	.....	.439	.678	.554	.466
E	.....	.....	.....	.460	.284	.304
F	.....	.....	.....	.....	.499	.484
G	.....	.....	.....	.....	.....	.241

NOTE.—The mean genetic distance between villages is .432 units.

Barandiaran (1961, 1962, 1966), Fuchs (1961, 1964), and Nothomb (1968). Reference to figure 1 of Gershowitz et al. (1970) will be useful in the following discussion.

Prior to 1910 the Makiritare appear to have existed as two subgroups, the Yekuana and Dekuana (Koch-Grünberg 1917), in the confluence of the headwaters of the Ventuari, Caura, and Padamo River systems. Intermittent warfare, accompanied by cannibalism, appears to have persisted between the two groups until the first decades of this century, with the Dekuana of the middle Ventuari and Caura temporarily gaining the upper hand before they became decimated by a series of epidemics some 35 years ago. The migratory movements of Makiritare villages subsequent to 1910 have been largely influenced by two factors—the importance of trading in Makiritare culture and the disruptive processes accompanying the contact of a primitive group with civilization. Of special importance in the latter context were the pressures resulting from the activities of the rubber tappers during the natural rubber boom (ca. 1910–1925). These pressures apparently led some villages on the periphery of the tribal distribution to retreat into the heartland in an effort to avoid the possibility of forced labor.

The Makiritare have seemingly "always" participated in the ancient trading net-

work that extended west as far as the Colombian Andes and east to the Atlantic border of the Guiana region. This trading network probably existed in pre-Columbian times (Reichel-Dolmatoff 1961; Evans 1964; Rouse 1964) and almost certainly increased in importance during the post-Columbian settlement of America. The role of the Makiritare in this network was traversing the Moné Pass between the Paragua and Caura River basins and plying the upper reaches of the Ventuari and Caura Rivers. Remnants of this traditional trading network persist today in the easterly movement of curare to the Makiritare from the Piaroa and westerly movement of guns and dogs from the Makushi, while the justly famous beadwork and basketry of the Makiritare passes in both directions. The mobility of trading parties appears to have markedly increased in the last 50 years. At the same time, there has been a definite movement of the Makiritare villages away from their ancestral areas, characterized by mountainous terrain and small rivers, into the larger river basins of the Ventuari, Cunucunuma, Padamo, and Erebato. A stated consideration in some of the relocations of villages to be described below has been to be closer to mission stations and their trade goods. Currently, small groups of Makiritare, mostly male, occasionally visit the little towns of the Venezuelan and Brazilian interior, both as market places for their goods and as places to earn money. In recent times, this has resulted in some Makiritare villages taking on the character of a "migrant" population, with a large proportion of the adult males absent from the village at any one time.

There is no doubt that the pressures from tappers during the rubber boom and then the location of missions in Makiritare country, the latter beginning some 15 years ago, have altered many aspects of Makiritare life. However, in their retreat into inaccessible areas under pressure from tappers and subsequent expansion into new areas as the pressures disappeared and new trading opportunities arose, we see a possible reenactment of a response that may have occurred repeatedly under different circumstances in pre-Columbian America. That the Makiritare have remained so relatively undisturbed, and hence have retained so much of their tribal structure, is undoubtedly related to the manner in which adjacent tribes such as the Arakuna and Máku, because of their location, buffered them against civilized influences.

We turn now to a detailed consideration of the antecedents of the seven villages we studied. Figure 1 is a diagrammatic summary of the events to be described. Some 60 years ago, as the complex of villages in the intermingled headwaters of the Cunucunuma-Ventuari-Caura River systems began to experience increasing pressures from the outside world, the population shifted into the more inaccessible areas of the region and complexes of related villages were found occupying the same general location. From one such complex, known as Wacamuña (comprising some four or five related villages), five out of the seven villages we have studied were derived. After the initial contraction, the general migratory movement was southeast into the area drained by the Merevari (an upper tributary of the Caura) and by the northwestern tributaries of the Rio Branco. Initially the migration was as integral village units. One village, which had originated in the Padamo-Cuntinamo area, migrated ahead of the others and moved down the Uraricoera River, a tributary of the Rio Branco, where a series of conflicts occurred with the Yanomama who originally inhabited the area (see Chagnon et al. 1970). As a result of the intense fighting, the Makiritare vil-

lage moved east into the Auraris River basin where it was joined by a band from the Kanarakuni area of the Caura. During the past 30 years, this village, now known as Juduaduña (A), has received a number of nuclear families from villages located in its point of origin in the Padamo-Cuntinamo area.

As the pressures from rubber tappers and settlers grew more intense in the period around 1920, some of the weaker villages fragmented and migrated as extended family units into the Merevari area. Here they reaggregated into the original units, but were joined by families migrating west from the Rio Branco area where fighting with the

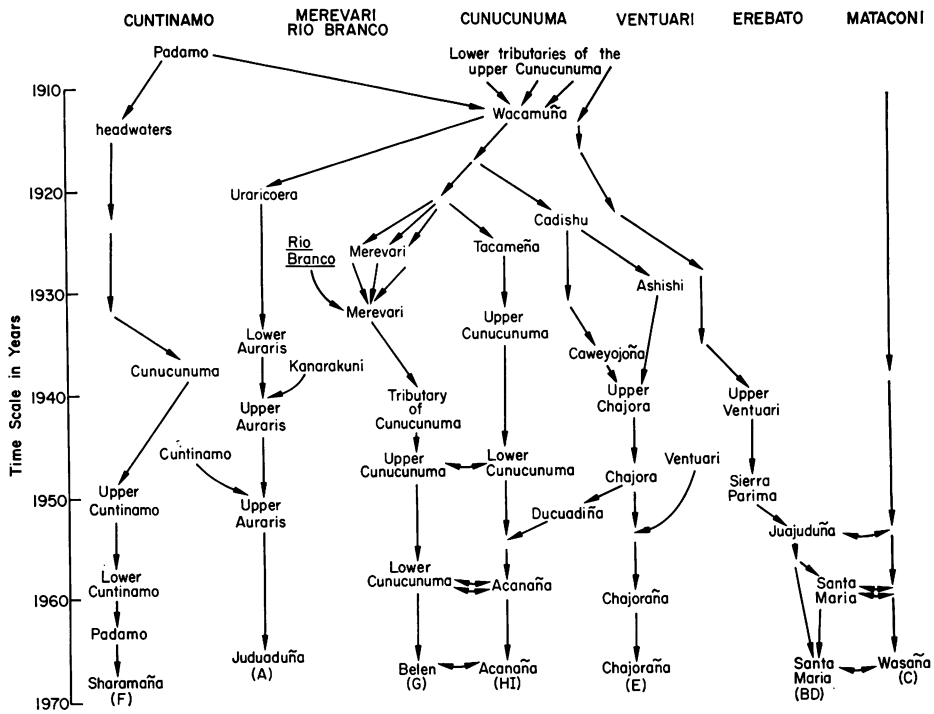

FIG. 1.—Diagram of the historical relationships and migration patterns during the past 60 years leading to the establishment of the seven Makiritare villages studied. The changing temporal-spatial relationships are indicated by reference to the time scale shown on the left and the six main geographical areas represented by the headings at the top.

Yanomama was intense. Eventually the village that was to become Belen (village G) moved back into the Cunucunuma headwaters with families from the Merevari area. This village slowly migrated into the lower Cunucunuma following its sister village, Acanaña (village HI). The present village site on the lower Cunucunuma was reached about 1960, when regular but intermittent contacts with non-Indians were established for the first time.

Acanaña (village HI), which had remained in the headwaters of the Cunucunuma at Tacameña, migrated out into the main Cunucunuma basin in 1940. It moved downstream to its present location in 1955, when permanent contact with a small mission was established.

Before the eastward migration occurred, part of the original Belen-Acanaña complex migrated west to Cadishu on the Cunucunuma, and 10 years later (1920) this village split into two groups, one going to Ashishi on one of the small tributaries of the higher Ventuari, the other remaining in Cadishu. The latter group subsequently migrated across the Ventuari basin to the upper Chajora River. Here they were later joined by the majority of the first group. In the next 20 years this village, Chajoraña (E), moved downstream, eventually reaching its present location, some two hours travel from the Erebato, 10 years ago. During the latter period, the village was joined by family groups migrating from the upper Ventuari. This process is still occurring to some extent. The only major split occurred 20 years ago when a family group migrated back into the Cunucunuma region to rejoin their relatives. This group is now part of Acanaña (HI) and has married extensively into Belen (G).

While other villages were moving out as described above, one of the strongest villages of the Wacamuña complex remained in situ in the Cunucunuma area, but then migrated to the upper Ventuari about 1935–1940. This village, forerunner of our BD, then moved east into the Sierra Parima area, and then north to Juajuduña on the Erebato River in about 1955. The village remained here until its chief's death, when it split into two groups; one group of 70 people moved down to the present site (Santa Maria) where their first permanent contact with civilization was made in 1959 (Barandiaran 1961). Later the remnant group moved out of the headwaters of the Erebato and joined them at this location, forming village BD.

The village of Wasaña (C) was formerly located on the upper Mataconi, where it remained relatively undisturbed by the perturbations of the period 1920–1940; after that it migrated into the Caura River system and began to form an alliance with the stronger village BD. Since 1955 there has been a high degree of intermarriage with village BD (see migration matrix below), although Wasaña still has no permanent contact with the outside world.

The village of Sharamaña (F) originated in the headwaters of the Padamo and was formerly closely allied to the antecedents of village A before the latter moved to Wacamuña. Except for a 10-year period of disruption, when the village migrated to the upper Cunucunuma, the village has remained in the Padamo River system and maintained its strongest ties with the villages at the headwaters of the Padamo and Cuntinamo Rivers. Recently, however, there has been an influx of migrant workers from Acanaña to work at the mission at Sharamaña.

In summary, the process of acculturation during the last 60 years appears to have brought about an increase in intervillage migration in the Makiritare, in an analogous fashion to the Xavante and other recently contacted tribes (Salzano et al. 1967). Apart from a general increase in village mobility, there have been three main effects of acculturation: (1) the disappearance of the formerly strong "Dekuana" from the Caura and lower Ventuari due to a series of epidemics (their place on the Caura has now been filled by the Yanomama); (2) a temporary increase in the intensity and occurrence of warfare between the Yanomama and Makiritare, as both tribes were pushed into closer conjunction (most fighting stopped some 10–20 years ago); and (3) fragmentation of villages into multiple extended family units which then migrated separately into another, not necessarily related village.

MIGRATION

The preceding section indicates a considerable amount of migration between villages during the last 60 years. Since a high degree of migration supposedly has a marked effect on the amount of random genetic drift, the degree of genetic microdifferentiation observed among the Makiritare is all the more notable. Accordingly, we wish now to investigate in detail the migration that has occurred in these seven villages over the last 60 years in light of the possible effect it might have on genetic microdifferentiation.

Among the various genetic models of population structure which have been proposed, the most realistic, from our standpoint, attempts to predict the variation in gene frequencies between colonies from a stochastic migration matrix (Bodmer and Cavalli-Sforza 1968). This model allows a continuously variable amount of migration between any two colonies, the colonies being of finite size and with no constraints upon their distribution in space. The model is formulated around a matrix of order K, which presents the observed displacement over one generation among k colonies, a colony in this instance being defined as any group that remains stable from one generation to the next. Such a migration matrix, where the ijth element represents the number of individuals born in colony i descended from parents born in colony j, can be formulated separately for mothers and fathers, or an average matrix can be derived for both sets of parents. From such an observed matrix, $\bar{M}$, stochastic matrices whose elements represent the transitional probabilities from one generation to the next can be derived. One, termed the forward migration matrix M^*, has elements m^*_{ij} denoting the probability that an individual born in colony j will go to colony i, while the elements m_{ij} of the backward migration matrix M denote the probability that individuals born in colony i have parents derived from colony j.

An important product of this model is the derivation from the backward matrix of the expected variances of the gene frequencies in the population under consideration. This derivation is based on the assumption that random sampling of genes leading to random genetic drift takes place in every colony in each generation after migration has occurred. We have previously emphasized that many of the processes leading to genetic differentiation in tribal populations are nonrandom (Neel and Salzano 1967). Here we shall restrict ourselves to evaluating the appropriateness of the stochastic matrices for the description of migration in such populations. The backward stochastic migration matrix, based on an observed migration matrix, is presented in table 3. The matrices for villages BD, E, G, and HI are thought to be as complete as possible, but the dispersion of village F into small groups because of a measles epidemic (see Neel et al. 1970) and the fact that contacts with village C were limited to that portion which could be persuaded to meet us on a river bank at two days walk from their village may result in the data for these villages being somewhat less complete. Only six villages are represented in the matrix, the seventh village (A) being separately represented as a row vector since we did not feel the genealogical information from this village, collected in 1967, was comparable to the information we had collected for the other series in 1968 and 1969. Otherwise stated, the correspondence between the elements of the row vector of table 4 and the column vectors of the matrix of table 3 is

somewhat uncertain, even though the same geographical labels have been used for easier reference to figure 1 in Gershowitz et al. (1970). In the discussion to follow, village A will be largely ignored except when we consider migration from non-Makiritare populations. Four points should be noted about the stochastic matrix in table 3.

1. Bodmer and Cavalli-Sforza have formally introduced a parameter to account for the stabilizing linear processes of selection, migration from the outside world, and mutation. This parameter, termed "migration from the outside," is denoted by a column vector α where the α_i element denotes the stabilizing effect the above pro-

TABLE 3

BACKWARD STOCHASTIC MIGRATION MATRIX FOR SIX MAKIRITARE VILLAGES

VILLAGE	N	$m_{.j}$						$\alpha_{.j}$						
		BD	C	E	F	G	HI	1	2	3	4	5	6	7
BD	368	.783	.079				.016	.060	.019				.038	.005*
C	128	.180	.774					.047						
E	166			.663			.018	.319						
F	138				.544		.029		.145	.080			.044	.159
G	188	.011		.005		.601	.011	.043		.075	.133	.080	.032	.011
HI	334				.003	.036	.560	.129	.090	.105	.045	.027		.006

NOTE.—Geographical designation of the $7\alpha_{.j}$ column vectors: 1, Ventuari; 2, Cuntinamo; 3, Padamo; 4, Cunucunuma; 5, Caura; 6, unknown; 7, Yanomama.

* Denotes one Venezuelan "campestino" who fathered two children in this village.

TABLE 4

BACKWARD STOCHASTIC MIGRATION VECTOR FOR VILLAGE A (JUDUADUÑA)

Village	N	A	1	2	3	4	5	6
A	154	.331	.331	.065	.130	.065	.013	.065

NOTE.—1, Cuntinamo; 2, Mataconi; 3, Kanarakuni; 4, Cunucunuma; 5, Padamo; 6, Yanomama.

cesses have on the ith colony. We will only consider the contribution of migration from the outside to these linear pressures, and have subdivided our α vector into seven column vectors, $\alpha_{.j}$ ($j = 1, \ldots, 7$), each corresponding to migration from a distinct area. Immigration from the outside can be evenly distributed to all k colonies (isotropic) or unevenly (nonisotropic). The above procedure of subdividing the α vector reveals that nonisotropic immigration from the outside can occur both as a function of the total value, $\alpha_{i.}$, for the ith colony and as a function of the distribution of the various α_{ij} components making up $\alpha_{i.}$ (we shall return to this point later). This procedure also facilitates the comparison of the migration matrix with the village histories (see above and fig. 1) and the genetic networks derived from the distance function (see below and fig. 2).

2. We have presented the average migration matrix by summing the data for fathers and mothers, yet we feel that in the Makiritare, as in all tribal societies, the

linear stabilizing forces and the transitional probabilities themselves are not the same in both sexes. This seems to be especially true for the α vector (see below). Undoubtedly the significance of this difference between the sexes is less important for modern human populations than for tribal societies where social constraints on marriage patterns will give rise to different probabilities of migration for each sex.

3. The probabilities are based on the total village population (four generations) rather than the single generation required by the model. Two reasons are adduced: (1) since human populations have continuous overlapping generations rather than discrete generations, most sets of data will approximate a generation by some subset of the colony at a point in time (we consider our genetic sample to be an appropriate subset); and (2) as we shall compare the stochastic matrices with the genetic networks (fig. 2) as well as with the histories, the comparison should be made on the same set of individuals.

4. We have distinguished between intratribal and intertribal migration in the α vectors by designating the $\alpha_{.7}$ column as migration into the Makiritare tribe from the Yanomama, their neighbors to the south. The frequency of such intertribal migration and its significance for genetic microdifferentiation will be discussed in later papers.

We now present the salient features of the comparison of the stochastic matrix (table 3) with the village histories.

1. The essential features of the village histories as recounted by our informants are confirmed by the migration matrix.

2. The close links established between villages BD and C are expressed in the highest off-diagonal, $m_{ij(i\neq j)}$, values in the matrix M, while the high degree of endogamy confirms the relative isolation of these two villages from the other four (a function of political strength in the case of village BD, and geographic isolation in the case of village C).

3. The $\alpha_{.1}$ vector, giving the transitional probabilities for migration from the Ventuari region, has the largest value for village E, and the second largest value for village HI, as expected. This high degree of isotropic migration from this sector of the "outside world" implies that these two villages should be genetically closer together than the m_{ij} elements of M would suggest. Figure 2 confirms this supposition.

4. The area of origin in the last 30 years can be accurately deduced for all those villages with $\alpha_{..} > 0.15$, Acanaña (HI) being the only exception, due to a high degree of migration from the Padamo ($\alpha_{.3}$).

5. Juduaduña (A) has many of the attributes of a refugee population, with a surprisingly low rate of endogamy and a high rate of migration from many different sources.

We now examine some of the attributes of our stochastic matrix in light of the requirements of Bodmer and Cavalli-Sforza's (1968) model. In order to consider the degree of distortion resulting from the derivation of the stochastic matrix from more than one generation, we have constructed discrete generations for each village, assigning every individual to one of four generations, each of approximately 20 years. With few exceptions (e.g., marriage across generations) the data corresponded closely to a model of discrete generations, with each generation extended across villages by virtue

of common ancestors existing prior to 1850 and marriage alliances since 1850. For each generation, a father-offspring and a mother-offspring backward matrix was constructed. The matrices for the second and third generations are shown in table 5. (The matrices for generations 1 and 4 are not displayed, since our information is least reliable for the former and individuals in the latter have not completed their migration.) From these matrices several points can be inferred:

1. *Stability.* The stability of the migration matrix represented in table 3 could not be tested in the manner advocated by Bodmer and Cavalli-Sforza (using the forward stochastic matrix), since possible underestimates of colony size (for villages C and F—see above) would give the same result as migrational instability by causing an apparent deviation between expected and actual colony size. We have, therefore, resorted to comparing the migration matrices for generations 2 and 3 as a test of migrational stability. Inspection of the matrix reveals marked instability in the elements of the four matrices, with m_{ij} and α_{ij} elements varying from one generation to the next. The most marked instability is for the diagonal elements $m_{ij(i=j)}$ where a sharp increase in endogamy is noted for villages E, F, G, HI; villages BD and C are more constant, with a decrease for Wasaña (C) in the mother-offspring matrix. This marked deviation from equilibrium of migration is at least partially due to a violation of one of the basic requirements of the migration matrix model in that the colonies are not stable units recognizable from one generation to the next. This factor obviously contributes to the marked instability of the $\alpha_{.j}$ vectors, since the formation of a new village from an old village would cause a marked shift from an α_{ij} element to an $m_{ij(i=j)}$ element, as observed in table 5. Since the majority of natural populations do not have temporally stable colonies, the formation of an equilibrium migration matrix, and hence a derivation of expected variances will only be possible in certain selected populations, such as the settled agrarian societies studied by Modiano et al. (1965). One way around this difficulty is to consider the probability of existence of the colonies. Thus the stochastic matrix would itself be embedded in a process of continuous probability flux. However, the specification of a function giving the probability density of the colonies and hence the form of the matrix is likely to be difficult. An alternative approach to the difficulty is to consider one generation only, but many more colonies so that an approximation to the equilibrium matrix is given.

2. *Isotropic migration.* Consideration of the $\alpha_{.j}$ vectors in table 5 indicates that migration from the outside is so markedly nonisotropic in time and space that it is unrealistic to present it as a single vector. This is partially a function of the instability of the colonies (see above), but not wholly, since the change in the Padamo vector for villages G and HI cannot be explained thus and neither can the changes in the $\alpha_{.7}$ vector be a consequence of colony existence. The magnitude of this effect is not only due to the physical displacement of colonies in space, but also to the changes in village alliances through time. It appears clear that the assumption of isotropic migration does not hold for this primitive population (or presumably for others), and furthermore the effect is great enough to contribute to a maintenance of the genetic diversity seen in such populations when found in conjunction with the fission-fusion type of population structure.

3. *Differences in mother-offspring and father-offspring matrices.* The two matrices

TABLE 5

BACKWARD MIGRATION MATRIX FOR GENERATION 2 AND GENERATION 3 IN SIX MAKIRITARE VILLAGES

VILLAGE AND N	$m_{.j}$						$\alpha_{.j}$							$\alpha_{..}$
	BD	C	E	F	G	HI	1	2	3	4	5	6	7	
	Father-Offspring Matrix													
BD:														
64	.766	.078					.047	.016				.063	.031*	.156
87	.782	.126				.012	.046					.035		.081
C:														
10	.200	.700					.100							.100
29	.241	.759												
E:														
14						.071	.929							.929
37			.838			.054	.108							.108
F:														
13				.077		.077		.462	.154				.231	.846
30				.700				.100	.067			.067	.067	.300
G:														
27					.222	.074	.074		.222	.259	.148			.704
49	.020		.020		.878		.041					.041		.082
HI:														
54					.037	.333	.167	.148	.148	.074	.093			.628
76				.013		.869	.026	.053		.040				.119
	Mother-Offspring Matrix													
BD:														
66	.788	.076					.076					.061		.136
87	.828	.081				.011	.046					.035		.081
C:														
10	.100	.800					.100							.100
29	.310	.690												
E:														
14							1.000							1.000
37			.757				.243							.243
F:														
13				.077		.077		.462	.154				.231	.846
30				.300		.067		.033	.133			.067	.400	.633
G:														
29					.345		.138		.138	.310	.069			.655
49					.735				.041		.184		.041	.265
HI:														
54					.056	.204	.333	.093	.278	.037				.741
76					.079	.868	.026	.013	.013					.053

NOTE.—The ijth transitional probabilities for the second generation are represented by the uppermost entry in the ij position, and the lowermost entry for the third generation. Geographical designations for the $\alpha_{.j}$ vectors are the same as in table 3, while $\alpha_{..}$ is the total probability of outside migration. Absence of an entry indicates zero migration.

* Venezuelan national.

derived for each generation are very similar in the m_{ij} elements. However, the linear stabilizing forces, as measured by the α_{ij} elements appear to be different for each sex. The most marked differences are seen in the $\alpha_{.7}$ vector, which corroborates the fact that in the Makiritare the probability of gene incorporation is dependent on the sex of the bearer, as in the Yanomama (e.g., Chagnon et al. 1970). The probability of a Yanomama woman contributing to the Makiritare gene pool is greater than that for a Yanomama male. Despite the differences in the α_{ij}, the average amount of migration within the tribe is approximately the same for both men and women, even though the males are expected to have a higher index of migration in such a matrilocal tribe.

4. *Equivalence with genome identity.* In order to ascertain whether the total migration matrix (tables 3, 4) accurately represents the degree of genetic identity that might be expected to obtain between the colonies on the basis of the genealogies, we have presented the distribution of gene origin in table 6. This method of analysis has

TABLE 6

MATRIX OF GENE IDENTITIES FOR SIX MAKIRITARE VILLAGES

VILLAGE	N	VILLAGES						GEOGRAPHICAL AREAS						
		BD	C	E	F	G	HI	1	2	3	4	5	6	7
BD	438	.624	.183	.....	.....	.....	.007	.085	.074	.....	.....	.....	.040	.007
C	170	.053	.924	.....	.....	.....	.....	.....	.024	.....	.....	.....	.....	.....
E	196	.....	.....	.....	.....	.....	.084	.916	.....	.....	.....	.....	.....	.....
F	146	.....	.....	.....	.243	.....	.027	.....	.394	.082	.....	.....	.069	.185
G	248	.040	.....	.020	.....	.295	.010	.080	.063	.133	.258	.057	.020	.025
HI	346	.....	.....	.....	.022	.075	.365	.257	.042	.147	.050	.041	.....	.003

NOTE.—N equals the number of genes; the ijth element indicates the proportion of genes in the ith village derived from the jth location. Geographical designations are the same as in table 3.

a resemblance to the concept of genetic homogeneity (Hiorns et al. 1969) and is carried out thus: as an individual enters the pedigree he is classified according to his origin, and he will contribute a score of 2 genes from that origin to his generation. His progeny will each contribute a score of 1 gene and their progeny a score of $\frac{1}{2}$ gene, and so on. Thus, if an individual in generation I came from the Ventuari and had six great grandchildren in generation IV, these six will contribute a total score of 1.5 from the Ventuari to their generation. This method is expected to give a close correspondence with the genetic network (as it does) and by taking into account nonrandom mating, differential fertility, etc. over several generations, it gives a closer approximation to what has transpired than the migration matrix from one generation.

The advantages of this method in showing the genetic effects of migration in such small populations can be demonstrated by considering the relationship between villages BD and C. Table 3 indicates approximately equal migration between the two villages, a fact at variance with the history which indicates that Wasaña (C) is migrating into the stronger village of Santa Maria (BD) to get trade goods. Table 6 indicates that the history is indeed correct. Inspection of the data, generation by generation, reveals the discrepancy to be due to marriage of Santa Maria males with Wasaña females, the resulting children (born in Wasaña, as marriage is matrilocal)

then coming to live and marry in Santa Maria. A similar situation arises for villages G and HI, table 6 giving a better representation of the historical events than table 3. A disadvantage of the method is that it requires great genealogical depth when colonies are temporally and spatially unstable. Thus the relationship of village E with villages G and HI is largely obscured, because our genealogies from village E were not sufficiently detailed.

5. *Nonrandom sampling of the gene pool.* The possible extent of the deviation from the required assumption of random processes operating after migration (necessary for the calculation of expected variances), due to the effects of nonisotropic migration coupled with differential fertility, nonrandom mating, etc., is illustrated in table 7, concerned with the probable survival of non-Makiritare genes in proportion to the population genome, generation by generation. The weaker (smaller) villages (e.g., A, F) appear to have a higher probability of incorporating foreign genes, and the effect is proportionately greater when it occurs. Furthermore, the frequency of foreign genes appears to decline with time. In this small sample, the phenomenon is due to the fact that the number of offspring reaching maturity is below average for immigrants and their descendants (presumably as a result of social selection). Thus, the establishment of foreign genes in the Makiritare may occur less frequently than in other tribes with different social structure (e.g., the Yanomama, see Chagnon et al. 1970).

TABLE 7

PROPORTION OF THE POPULATION GENOME OF SEVEN MAKIRITARE VILLAGES THAT IS DERIVED FROM A NON-MAKIRITARE POPULATION (YANOMAMA), ANALYZED BY GENERATION

GENERATION	VILLAGE						
	A	BD*	C	E	F	G	HI
1	.000	.000	.000	—	—	.000	.000
2	.037	.013	.000	.000	.250	.046	.000
3	.152	.004	.000	.000	.229	.019	.007
4	.000	.000	.000	.000	.096	.063	.000
Total	.061	.007	.000	.000	.185	.025	.003

NOTE.—The column totals give the total amount of gene admixture in a village (see table 6). The (—) indicates inadequate information.

* The non-Makiritare genes in village BD were contributed by a Venezuelan national.

In conclusion, while the model of Bodmer and Cavalli-Sforza gives the nearest approach to the realities of migration, the Makiritare depart in a number of significant aspects from the assumptions necessary to predict variation in gene frequencies.

1. Sampling of genes for the next generation, after migration, is nonrandom (e.g., table 7).

2. Colonies are not stable units, constant from one generation to the next (e.g., table 5).

3. The degree of nonisotropic migration, temporally and spatially, appears so high that it is unrealistic to present it as a single linear stabilizing factor (table 5).

4. The procedure of obtaining the observed matrix can result in a distortion from the real migratory situation (table 6).

The extent to which these departures affect the predictive value of their model will be explored in later papers.

Neel (1969) has suggested that, by contrast with settled agricultural populations, the demes of primitive tribal populations were characterized by a relatively stronger interplay between dispersive and stabilizing genetic forces. The data of the last two sections now begin to provide concrete documentation for that point of view. The data also suggest that few if any villages (the ultimate breeding unit) can possibly be in "genetic equilibrium." In fact, while we hesitate to generalize, one can speculate that with this population structure, the classical concept of genetic equilibrium can never be more than a convenient fiction. Conversely, with the probability that throughout the course of human evolution there has been similar deme disequilibrium, one is driven to question formulations of the extent of the genetic load subsumed by human populations when such formulations are based upon a hypothetical state of equilibrium never remotely approached.

GENETIC NETWORKS

Utilizing the genetic distances presented previously, we have constructed three genetic networks which we propose to evaluate pragmatically by comparison with the village histories and migration matrices presented. While various procedures may be used to generate such networks, the initial input of genetic distances assumes a greater significance in determining the final form of the network than does the method used to obtain it (Fitch and Neel 1969; Kidd and Sgaramella, personal communication, 1970). We have therefore continued to use the approach of Cavalli-Sforza and Edwards (1964, 1967) as it is probably the most widely known method. Their method consists of developing a "KN matrix" from the results of an initial cluster analysis and using an algorithm to find the "best" network. In this instance, we have used a modified form of an algorithm supplied by Edwards, the criterion for the "best" network being that which has minimum net length, although other criteria are available (Cavalli-Sforza and Edwards 1967; Kidd 1969). Rather than examine all 945 networks for each set of distances to ensure choosing the single network with minimum net length in each instance, we chose as the "best" that network which diminished by less than 0.00001 in total net length from all previous trees derived from the original cluster analysis. Such a network was typically found after examining 30–40 networks subsequent to the topology based on the cluster analysis. Any differences in topology between the networks depicted here and the network with absolute minimum net length are likely to be small (Kidd 1969; Kidd and Sgaramella, personal communication, 1970).

The three networks derived from the three distance matrices are shown in figure 2. They are drawn to scale, plotted on polar coordinates with genetic distance measured along the radii. In an attempt to show the different amounts of dispersion graphically, the populations have been plotted on the same radii in each figure wherever possible. Consideration of the three figures reveals the following points:

a) The "best" network found, using the set of six loci (Rh, MNSs, Duffy, Kidd,

Diego, and haptoglobin) (fig. 2*a*), appears quite distinct from the network found using the distances derived from the set of five loci (P, Lewis, Gc, PGM_1, and acid phosphatase) (fig. 2*b*) in several important respects. The most important difference is the radical change in placement of village BD; the relationships of village HI are also different in the two figures.

b) The network derived from all 11 loci combined (fig. 2*c*) differs from the previous two in two important respects. There are no zero segments and the sum of

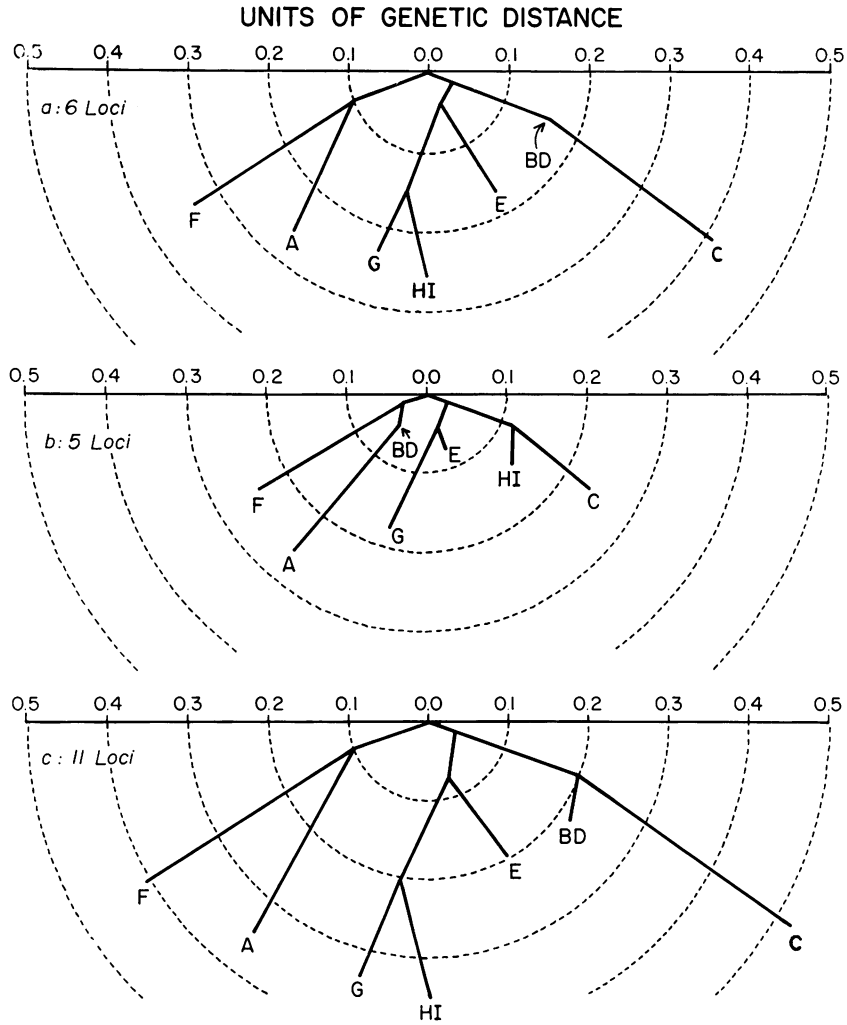

FIG. 2.—Genetic networks derived from the pairwise distances in tables 1 and 2: (a) six loci—Rh MNSs, Duffy, Kidd, Diego, and haptoglobin (total net length = 1.3885); (b) five loci—P, Lewis secretor, Gc, acid phosphatase, and PGM_1 (total net length = 0.9092); (c) 11 loci (total net length = 1.7473). The networks are plotted to scale on polar coordinates with units of genetic distance read along the radius of the diagram.

the vectors connecting the nodes is greater, implying a more stable configuration. As discussed previously, an increased number of loci appears more likely to reflect the true genetic distance between populations; in addition a more stable network results. This network differs only slightly in arrangement of the villages from that given by six loci, but the dispersion is much greater.

c) The correspondence between the village histories as shown in figure 1 and migration matrices, on the one hand, and the genetic network derived from all 11 loci (fig. 2*c*), on the other, is excellent, while that with the 6 loci (fig. 2*a*) may be termed reasonable. In keeping with the history, villages A and F cluster together but are more separated than comparable villages with high rates of exchange, such as G and HI; that is, A and F illustrate the result of a fission with little subsequent exchange. The four villages most recently derived from the Wacamuña complex are also clustered closely together, with, however, village BD represented on the branch leading to village C. The association of these two villages in such a fashion within the network results from a form of hybridization, since the histories indicate that villages BD and C did not have a common origin during the time we are concerned with. The implications of such events for phylogenetic interpretations are discussed below.

d) The original method of Edwards and Cavalli-Sforza (1964) was developed in order to obtain a phylogenetic tree connecting the populations in a fashion representing the most probable course taken by evolution. However, as they indicate, the use of such networks as a best estimator of a phylogenetic sequence, leading to the representation of the resulting "best" network as the phylogeny, is based on the assumption that factors such as hybridization, convergence, and parallelism which give rise to loops in the phylogenetic tree are absent or infrequent. Our data on migration indicate that this is not a realistic assumption for this population. Two factors which result in an increased degree of genetic similarity in the "now plane" and hence in a distortion of the phylogenetic relationships are indicated by the data: (1) extensive intervillage migration, as in the case of village BD and C (hybridization), and (2) a high degree of migration from the same "outside" source for a pair of villages, as exemplified by the influence of the Ventuari vector (table 3, $\alpha_{.1}$) on villages E and HI (convergence). The present data provide a first test of the "robustness" of this approach in the face of departures from the assumptions; the results of the 11-locus approach suggest that the method will provide valuable data even in the face of considerable departures from the assumptions.

As a general principle, different networks resulting from different sets of loci will arise from an interaction of stochastic processes with the differing amounts and type of selection acting at each locus. In this particular instance, since a more reliable network is given by the Rh-MNSs-Fy-Kidd-Diego-Hp loci, we may speculate that the different configuration derived from the set of the other five loci indicates that the selective forces acting on that part of the genome represented by these loci (P, Lewis secretor, Gc, PGM_1, acid phosphatase) combine to produce an increased genetic similarity between village BD and village A, and between village C and village HI. Alternatively, of course, especially without variances, we can attribute this distortion to the operation of chance. Another way to evaluate the magnitude of possible bias introduced by the action of selection is indicated by a consideration of the genetic

distances derived on a single locus basis. We have already shown that the mean intervillage distance for six loci (Rh, MNSs, Duffy, Kidd, Diego, haptoglobin) in the Makiritare and Yanomama is 92% and 85%, respectively, of the mean intertribal distance based on the same set of loci for 12 South American tribes (Neel and Ward 1970). If this amount of genetic divergence results from the action of genetic drift upon independent loci, then the expected mean distance of each locus within a tribe will be 92% or 85%, respectively, of the mean intertribal distance for that locus, departures from expectation (i.e., the variance) being determined by the random walk of gene frequencies in successive generations. The relationship should still be approximated even if directional selection exists for some loci, provided it is constant in space. If variable selection occurs at a locus, then one of three possibilities may obtain: (a) if the intensity of "selective drift" (Kimura 1954) is the same for tribes and

TABLE 8

COMPARISON OF MEAN INTERTRIBAL GENETIC DISTANCE (12 SOUTH AMERICAN TRIBES) WITH MEAN INTERVILLAGE DISTANCE (MAKIRITARE AND YANOMAMA TRIBES) FOR SIX LOCI

Locus	Mean Genetic Distance		
	Intertribal ($N=12$)	Intervillage	
		Makiritare ($N=7$)	Yanomama ($N=7$)
Rh.....	.226	.121 (54%)	.149 (66%)
MNSs.....	.151	.192 (127%)	.172 (114%)
Duffy.....	.093	.050 (54%)	.052 (56%)
Kidd.....	.097	.074 (76%)	.152 (157%)
Diego.....	.128	.164 (128%)	— —
Hapto-globin....	.115	.124 (109%)	.120 (104%)

NOTE.—The expected proportions were 92% and 85%, respectively. The (—) indicates inadequate information.

villages, no differences in mean distance will result; (b) if the intensity of stabilizing selection versus random drift or random drift versus "selective drift" is greater within a tribe than between tribes, then the mean intervillage distance will be less than expected for the locus involved; or (c) conversely, if the proportion of "selective drift" versus random drift or random drift versus stabilizing selection is greater within a tribe than between tribes, the mean intervillage distance will be greater than expected, for that locus. The mean genetic distance for each of these six loci is presented in table 8 for 12 South American tribes and the villages of the Makiritare and Yanomama tribes. Since thus far an expected variance has not been derived for this distribution, we cannot attach significance values to the observed differences and at this juncture wish only to make three points: (1) most loci (Rh, MN, Duffy, and haptoglobin) exhibit consistent behavior in the two tribes but one (Kidd) does not; (2) the distribution of the "consistent" loci indicates a lesser or greater contribution to distance than anticipated from the tribal results under the assumption of no selection,

which would imply the existence of differential selection at some loci (see Sanghvi 1966); and (3) the lack of consistency with reference to Kidd, if not due to random walk, may be explained either by the action of uniformly distributed greater selective pressures in the Makiritare or by large differences in selective pressures from village to village in the Yanomama. The much more extensive data now becoming available for the latter tribe will permit an in-depth approach to these patterns of variability.

TOWARD A NEW MEASURE OF POPULATION ISOLATION

One of the basic parameters in the theoretical structure of population genetics has been the degree of isolation of a population (however defined) and its converse, migration between populations. Recent efforts to refine the treatment of isolation have tended to follow the elegant formulations of Malécot (1948 et seq.) and Kimura and Weiss (1964), where the isolation of a community is often measured as a function of geographic distance between the birthplace of husband and wife or parent and offspring. This development of the subject undoubtedly stems from the ease with which such data are collected, as well as from Wright's early formulations (1943, 1946). However, a moment's reflection reveals the severe limitations of this approach as an insight into the genetic significance of migration. In a large and relatively homogeneous population, such as that of Japan, the genetic distance between subpopulations or demes is likely to be small, so that the arrival of migrants from even a considerable geographic distance may have relatively little qualitative impact on the gene pool of the recipient population. Exchange of members between groups identical in their genetic composition has no more genetic significance than intragroup mating. Conversely, in an area where populations exhibit marked genetic microdifferentiation, such as New Guinea (Simmons et al. 1961 et seq.; Giles et al. 1966), even short geographic distances may correspond to relatively large genetic distances. Furthermore, the concept of isolation by distance breaks down completely in tribal populations such as the Makiritare and Yanomama Indians, where village sites are shifted frequently, for here potential marital partners whose birth places are separated by a considerable distance may find themselves in reasonable proximity when nubile, and vice versa. Parent and offspring may be born many miles apart and yet be members of the same (wandering) village. An approach unsuitable for application to the conditions under which man evolved would seem to need some revision.

In this section we shall suggest a simple way of expressing the genetic significance of migration, based on the frequency of migration and the genetic distance between the populations concerned. While this approach is substantially more demanding than employing a geographic distance function, the effort seems justified by the additional insights afforded. Table 9 is based on grouping the proportions in table 3 according to the genetic distances of table 2, with distances grouped in intervals of 0.1. For this purpose each entry in table 3 has been weighted by the village size according to its contribution to the total migration matrix, the weighted values of course summing to 1.0. For column 7 of table 3, involving intermarriage with Yanomama, we have calculated genetic distances as: from F, .615; from G, .742; and from HI, .768, employing the mean Yanomama gene frequencies derived from the data of Arends et al. (1967). As noted earlier, two children in BD are known to have been fathered by a Venezuelan

"campestino." From the observation that genetic distance between an Indian village and the tribal remainder is some 60% of that between Indian tribes, and genetic distance between Indian tribes about half that between major ethnic groups (Neel and Ward 1970), we shall somewhat arbitrarily, on the basis of table 2, assign this man a distance of 1.0, hoping to improve the data later.

The results might be expressed as a histogram. In a completely endogamous community, the histogram would be reduced to a single column centered on zero distance. The larger the off-zero entries and the further to the right they fall, the more genetically significant the migration. Two populations can be compared on the basis of the shape of their histograms, provided, of course, the genetic distances of the abscissa are computed in the same fashion and based on the same loci. A persistent problem in

TABLE 9

PROPORTION OF MIGRANTS OF TABLE 3 TABULATED BY GENETIC DISTANCE OF THEIR VILLAGE FROM THE RECIPIENT VILLAGE

Genetic Distance between Village of Origin of Parents and Village of Birth of Child	Proportion of Backward Migration Matrix
.00	.660
.00–.10	.....
.000–.100	.....
.100–.200	.....
.200–.300	.011
.300–.400	.048
.400–.500	.004
.500–.600	.....
.600–.700	.017
.700–.800	.003
.800–.900	.....
.900–1.000	.002
Unknown	.256

a treatment of this type will be the occurrence in the migration matrix of individuals from demes not yet studied, for which no gene frequency data are available. In this matrix, such persons represent .26 of the total. In this instance, some of the villages of origin probably no longer exist as such (cols. 1, 2, tables 3–6), so that no amount of field work would dispel the uncertainty. On the other hand, for approximately .15 of the matrix, data could be collected. One way to meet this issue is by arbitrarily assigning this "unknown distance" group a genetic distance from the recipient villages corresponding to the mean distance between all villages studied, in this case, .432. However, if the proportion of this group is sufficiently large (as here), the shape of the distribution might thereby be distorted. An alternative approach is to distribute this entry proportionately over the other Makiritare entries for which distance is known. The level of "distance unknown" at which this latter procedure becomes unwise is yet to be determined.

The data of table 9 can be reduced to an index of genetic isolation by multiplying

the proportions of column 2 by the midpoint of the distance intervals of column 1 and summing the products, assigning in this instance the unknown distance group to the interval .401–.500. In this case the index is .151. Data on other populations from which to manufacture comparable indices are not yet available, but it seems likely this will prove to be a high index. While convenient, the index fails to catch some of the nuances of the situation, such as modality; this can be accomplished by computing the higher moments of the distribution.

This index is a measure of the potentiality for changes in gene frequency resulting from inter-deme migration. Where the source of the migrants is limited to one or two villages, a relatively high index implies that the migrants will effect changes in the gene pool of the recipient village. However, where the migration matrix involves numerous villages and there is marked microdifferentiation, as in the case of the Makiritare, the vectors of gene-frequency change for specific loci associated with specific villages could conceivably be in opposing directions, with the vectors in effect cancelling each other. In a subsequent paper, we will undertake a locus-by-locus analysis of the effects of migration, with an eye to determining the precise extent to which the potential for change expressed by the relatively high indices of tribal populations is actually realized.

SUMMARY

Genetic distances between seven Makiritare villages based on (*a*) six loci (Rh, MNSs, Kidd, Duffy, Diego, and haptoglobin), (*b*) five different loci (P, Lewis secretor, Gc, erythrocyte acid phosphatase, and PGM_1), and (*c*) all 11 of these loci are presented. The village histories are then detailed, and a migration matrix of the Bodmer and Cavalli-Sforza (1968) type derived. It is shown that the actual behavior of these villages contravenes the assumptions necessary to the use of these matrices as visualized by Bodmer and Cavalli-Sforza. A genetic network (phylogeny) connecting the villages is derived by the technique of Edwards and Cavalli-Sforza (1964). The network based on the six and on all 11 loci agrees well with the historical data, but the five-locus network fits less well. The distorting effect of a large amount of exchange between two villages on the phylogenetic interpretation of such networks is shown. However, this technique may be useful in deriving a first approximation to the relationships of small population units where histories are less adequate than in this case, the reliability of the result being proportional to the number of systems studied. Finally it is shown that treatments which equate genetic isolation to geographic distance functions break down in populations of this nature. A new, simple approach to quantitating the genetic significance of migration is suggested.

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