MULTIPLE-LOCUS DEPARTURES FROM PANMICTIC EQUILIBRIUM WITHIN AND BETWEEN VILLAGE GENE POOLS OF AMERINDIAN TRIBES AT DIFFERENT STAGES OF AGGLOMERATION

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ABSTRACT

A comparative analysis of departures from multiple-locus Hardy-Weinberg equilibrium is presented for a set of four tribal Indian groups (the Yanomama, Makiritare, Wapishana and Ticuna) from the lowlands of South America. These tribes span a range of agglomeration and acculturation from the most traditional, swidden horticulturalists to frontier townspeople. The small-group social organization typical of traditional horticulturalists leads to substantial departures from tribal panmixia, as manifested by the distribution of multiple-locus genotypes both within and between villages. Within villages, the departures from single-locus Hardy-Weinberg equilibrium are small and nonsignificant, but the departures from gametic equilibrium (independence of loci) are substantial, even for the unlinked loci we have used to characterize these populations. The departures from single-locus homogeneity across villages are also substantial. One of the normal concomitants of increasing acculturation in this setting is an increase in agglomeration. As agglomeration increases, the departures from multiple-locus panmixia decrease, a process that can be very rapid. We discuss both the shifting balance theory of evolution and punctuated evolutionary rates in light of the small group social organization that must have obtained throughout most of human evolution.

FOR the past 20 years, beginning with our studies of the Xavante Indians of the Brazilian Mato Grosso (NEEL et al. 1964; SALZANO, NEEL and MAYBURY-LEWIS 1967), we have carried out a series of studies on the genetic organization and social structure of South and Central American Indian tribes. The primary motivation for this ongoing research has been the belief that it should be possible to determine the extent to which the genetic organization of these human populations reflects their social organization, demography and ecology. Two aspects of genetic organization have emerged. First, the random influences on these generally small populations are sufficient to generate substantial microdifferentiation among villages within a tribe, as measured either by F-statistics (NEEL and WARD 1972) or by analogous treatments (SPIELMAN, NEEL and Li 1977). This pattern of infratribal differentiation is a general finding in our studies (cf. NEEL et al. 1977a,b; SALZANO et al. 1977; SMOUSE and WARD 1978), as well as in the studies of others on tribal groups from around the world.
(cf. Giles, Walsh and Bradley 1966; Giles, Wyber and Walsh 1970; Kirk et al. 1971; Friedlaender 1975; Szathmary and Ossenberg 1978; Wood et al. 1982). Second, the usual fission-fusion mode of village formation in tribal groups (Giles, Walsh and Bradley 1966; Neel 1967; Chagnon 1968, 1975, 1979a; Fix 1975, 1978, 1979; Smouse, Vitzthum and Neel 1981; Smouse 1982), when coupled with this microdifferentiation, should lead to systematic departures from genetic equilibrium within single villages (e.g., Nei and Li 1973; Sinnock 1975; Feldman and Christiansen 1975). We have demonstrated that this is indeed the case for the Yanomama (Smouse and Neel 1977; Smouse 1982).

One of the usual concomitants of increasing acculturation in this region is an increase in agglomeration (increasing community size), and community size is the critical variable in most of what follows. In this paper we consider the relationship between the level of tribal agglomeration and random departures from multiple-locus panmictic equilibrium. Having demonstrated the extent to which these departures depend on village size, we will suggest (1) that the principal influence on unacculturated tribal gene pools is stochastic in nature, a fact that has some potentially profound implications for human evolution, (2) that the breakdown of normal tribal genetic structure is both dramatic and extremely rapid during the agglomerative phase of acculturation and (3) that the evolutionary forces governing modern cosmopolitan populations are substantially different from those that must be applied among our tribal predecessors. Although none of these observations is entirely novel, the extent to which they are supported by our results is striking.

POPULATIONS STUDIED AND GENETIC LOCI ANALYZED

The analysis we describe could easily be applied to any of the populations we have sampled, but we focus here on four groups spanning the range of acculturation (and agglomeration) found among tribal Amerindians from lowland South America; this set of tribes ought to provide some revealing contrasts. These tribes can be thought of as representing a continuum in acculturation, and we can study the acculturation (agglomeration) process by comparing their respective genetic architectures.

The Yanomama: The Yanomama are the least acculturated group we have studied and, thus, represent one extreme of the modernization continuum. The culture of this group has been described elsewhere (cf. Chagnon 1967, 1968, 1974, 1975, 1979a,b; Chagnon et al. 1970; Ward 1972), and we comment here on only two cultural features. First, villages are quite small ($50 < N < 250$) and well separated in space, so that the gene pools are relatively discrete (Neel and Ward 1972; Li and Neel 1974; Chagnon 1968, 1975, 1979a; Smouse and Neel 1977). Second, fission-fusion dynamics are prominent in this tribe (Smouse, Vitzthum and Neel 1981), a situation that should lead to substantial amounts of microdifferentiation and large amounts of disequilibrium between loci (Nei and Li 1973; Sinnock 1975; Feldman and Christiansen 1975). We have already reported a partial set of $F$-statistics (Neel and Ward 1972) and a set of disequilibria (Smouse and Neel 1977) for this group, but we repeat and extend some of those results here to facilitate comparison with the other groups. We
use 12 villages of the Yanomam dialect cluster (SMOUSE, VITZTHUM and NEEL 1981), which includes the Parima and Yanam groups of SMOUSE and NEEL (1977). Because of the extreme geographical subdivision of the Yanomama, this subtribal cluster is comparable to the totality of most other tribes. (Dialect clusters in the Yanomama differ from one another linguistically and genetically as much as do tribes in other language families, and to use the whole tribe would be to exaggerate the differences between villages.)

The Makiritare (Ye'cuana): Although almost as remotely situated as the Yanomama, the Makiritare exhibit a propensity to engage in extensive travel and trade and have been in contact with non-Indians for many more than a hundred years. They were under considerable territorial pressure during the days of the rubber boom and more recently have seen portions of their traditional territory invaded by settlers (ARVELLO-JIMENEZ 1971). Their efforts to reach a political accommodation with their present circumstances appear to have increased the amount of intervillage gene flow in recent years (WARD and NEEL 1970; SMOUSE and WARD 1978), although similar periods of increased genetic exchange between villages may have occurred in the past under pressure from other Indian groups. They are certainly more acculturated than the Yanomama, but tribal structure is essentially intact (ARVELLO-JIMENEZ 1971), and there is little evidence of non-Indian contribution to the present gene pool (ARENDS et al. 1970; GERSHOWITZ et al. 1970; WIEITKAMP and NEEL 1970). We use 11 villages defined by SMOUSE and WARD (1978), deleting only village lox, which is poorly sampled and not well characterized.

The Wapishana: The Wapishana have been in increasingly frequent contact with neo-Brazilians in the last 200 years, both as ranch hands and as subsistence farmers (NEEL et al. 1977a,b), and are well into their demographic transition (SALZANO, CALLEGARI-JACQUES and NEEL 1980a), but their settlements are still small (50 < N < 150). They have absorbed several neighboring tribes in the process of becoming acculturated (FARABEE 1918; RIVET 1924; LAYRISSE and WILBERT 1966), have received quite a few immigrants from the neighboring Macushi, and have incorporated a modest component of non-Indian admixture as well, about 5–6% of their gene pool being non-Indian in origin (NEEL et al. 1977b; SALZANO, CALLEGARI-JACQUES and NEEL 1980a). We have reduced the impact of recent immigration by removing from the sample all of the individuals who are aware of their non-Indian admixture or whose ABO or Gm types are not normally present in Amerindian populations, but we cannot completely remove all of the consequences of earlier immigration. This decision to “clean up” the gene pool is somewhat arbitrary but is compatible with our primary interest in the implications of acculturation and agglomeration. Interracial admixture has its own implications for the genetic structure of these populations, but that is an issue to be avoided here as much as possible. We report data on ten villages, deleting from the list of NEEL et al. (1977b) only 27C, which is poorly sampled.

The Ticuna: This tribe traditionally occupied many small villages along the tributaries of the Solimoes (Amazon) River near the border of Brazil, Columbia and Peru (NIMUENDAJÚ 1952; CARDOSO DE OLIVERIA 1977). They have recently
moved out of the interior, establishing settlements immediately adjacent to the Solimões, where they now occupy towns of 500-2000 inhabitants, some of which contain partially integrated neo-Brazilian minorities (Salzano, Callegari-Jacques and Neel 1980b; Neel et al. 1980). Traffic along the river is heavy, and these people (although still containing only about 2% non-Indian genes) are basically frontier townspeople (Salzano, Callegari-Jacques and Neel 1980b). Traditional social and kinship organizations are already breaking down, and although sufficient time has not passed since agglomeration to attain equilibrium, the Ticuna are well on the way to panmixia (Neel et al. 1980; Salzano, Callegari-Jacques and Neel 1980b). We use seven villages from the list reported by Neel et al. (1980), deleting only 371, about which we are in some doubt as to population size.

We have restricted attention to five unlinked, codominant loci in order to provide a measure of comparability across tribes, although additional such loci were typed in the Makiritare, Wapishana and Ticuna. The MN, Hp and Gc loci have been used for all four tribes. We have used RhE for the Yanomama but RhC for the other three tribes, choosing the more polymorphic of this highly correlated pair of markers in each case. We have used Alb for the Yanomama but PGM1 for the other three tribes, because PGM1 is largely monomorphic in the Yanomama, whereas Alb is largely monomorphic elsewhere. In view of the fact that RhC and RhE, being almost absolutely linked, are almost perfectly correlated, we are inclined to view RhC and RhE as statistically interchangeable and have chosen A1b and PGM1 to be as similar as possible in levels of polymorphism. We believe the loci selected for the four tribes are as comparable as we can make them. Our comparisons implicitly assume that the same forces are operative on all of these loci.

DEPARTURES FROM PANMIXIA

The model: Multiple-locus panmixia implies Hardy-Weinberg frequencies at each locus and independent segregation between loci (gametic equilibrium). We wish to gauge departures from either or both of these conditions. We begin by defining a genetic scoring convention for a pair of alleles at each locus, as shown in Table 1 for two loci (A and B). A multiple-allelic analog is available (Smouse 1979; Smouse and Williams 1982) but is not needed here. Under panmixia, the means of the variables are simply the allele frequencies, whereas the covariance matrix is \( \Sigma = \text{diag}(p_k(1 - p_k)/2) \). A generalized departure from panmixia does not change the mean vector, which takes the form

\[
U' = (\mu_A, \mu_B, \ldots, \mu_K)
\]

but does alter the covariance matrix to the form \( \Sigma = A'WA \), where

\[
W = 1/2 \begin{bmatrix}
p_A(1 - p_A) & D_{AB} & \cdots & D_{AK} \\
D_{BA} & p_B(1 - p_B) & \cdots & D_{BK} \\
& \ddots & \ddots & \ddots \\
& \ddots & \ddots & \ddots \\
D_{KA} & D_{KB} & \cdots & p_K(1 - p_K)
\end{bmatrix}
\]
DEPARTURES FROM PANMIXIA

**TABLE 1**

<table>
<thead>
<tr>
<th>Genotype</th>
<th>A locus genotypes</th>
<th>B locus genotypes</th>
<th>P_b + \theta_b P_b Q_b</th>
<th>2P_b Q_b (1 - \theta_b)</th>
<th>Q_b^2 + \theta_b P_b Q_b</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(A_1A_1)</td>
<td>(A_1A_2)</td>
<td>(A_2A_2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B_1B_1)</td>
<td>(Y_A = 1)</td>
<td>(Y_A = 1/2)</td>
<td>(Y_A = 0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Y_B = 1)</td>
<td>(Y_B = 1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B_1B_2)</td>
<td>(Y_A = 1)</td>
<td>(Y_A = 1/2)</td>
<td>(Y_A = 0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Y_B = 1/2)</td>
<td>(Y_B = 1/2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B_2B_2)</td>
<td>(Y_A = 1)</td>
<td>(Y_A = 1/2)</td>
<td>(Y_A = 0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(Y_B = 0)</td>
<td>(Y_B = 0)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Where

\[ u_A = f(A) = P_A \quad u_B = f(B) = P_B \]

\[ \Sigma = (1/2) \text{diag}(1 + \theta_b^{1/2}) \cdot \begin{bmatrix} P_A Q_A & D_{AB} \\ D_{AB} & P_b Q_b \end{bmatrix} \cdot \text{diag}(1 + \theta_b^{1/2}) \]

The \(D_{kl} = (P_{kl} - P_k P_l)\) are the gametic disequilibria (covariances) between the alleles at a pair of loci. The matrix \(A' = A = \text{diag}((1 + \theta_b)^{1/2})\) measures the departure from random union of gametes, and \(\theta_b\) for the kth locus is essentially \(F_{TS}\) of Neel and Ward (1972). It is possible to contrive examples with random union of disequilibrated gametes, i.e., where \(\theta_b = 0\) for all \(k\), but \((D_{kl} \neq 0: k, l = A, \ldots, K)\). We capitalize on this possibility later in our sequential hypothesis testing scheme.

In general, we expect both \(\theta_b\) and \(D_{kl}\) to be nonzero. An analysis of \(F\)-statistics usually ignores \(D_{kl}\) (cf. Neel and Ward 1972), whereas our earlier analysis of disequilibrium in the Yanomama ignored \(\theta_k\) (Smouse and Neel 1977). We propose a more complete estimation strategy here, based on the approximation of a genetic multinomial distribution to a multivariate normal distribution, an analysis that extracts both sorts of measures. Weir and his colleagues have also described estimation procedures for both measures (e.g. Cockerham and Weir 1977; Weir 1979; Laurie-Ahlberg and Weir 1979), and our procedure leads to a multivariate analog of their composite measures for one- and two-locus departures from panmixia. In particular, our \(D_{kl}\) is their \(\Delta_{kl}\).

The hypotheses: Let the genotypic vector for the \(j\)th individual be represented by \(Y_j' = (Y_{Aj}, Y_{Bj}, \ldots, Y_{Kj})\). Each genotype in our two-allele systems is capable of assuming values of 1, \(\frac{1}{2}\), and 0. For example, the genotype \((A_1A_2B_1B_2C_2D_2)\) is represented by \(Y' = (\frac{1}{2}, 1, 0, \frac{1}{2})\). We assume that the \(Y\) vectors are drawn from
a multinomial distribution whose large sample approximation is the multivariate normal distribution with mean vector \( \mathbf{U} \) and covariance matrix \( \Sigma \):

\[
f(Y_j) = \frac{|\Sigma|^{-1/2}}{(2\pi)^{K/2}} \exp[-(Y_j - \mathbf{U})\Sigma^{-1}(Y_j - \mathbf{U})/2]
\]

The assumption of multivariate normality cannot be taken too literally for finite samples, of course, but it leads to a simple and appealing estimation and testing framework (cf. Anderson 1958). Moreover, given even as few as five or six loci, the procedures to be described here are quite robust to violations of the normality assumptions (see Smouse and Neel 1977; Smouse, Spielman and Park 1982; J. C. Long and P. E. Smouse, unpublished results).

The next step is to construct a series of hypotheses that lead to the analysis we require

\[
H_0: \mathbf{U} = \mathbf{P} \text{ and } \Sigma = \Gamma \\
H_1: \mathbf{U} = \mathbf{P} \text{ and } \Sigma = \Gamma + \mathbf{D} = \mathbf{W} \\
H_2: \mathbf{U} = \mathbf{P} \text{ and } \Sigma = \mathbf{A}'\mathbf{W}\mathbf{A}
\]

where \( \Gamma = \text{diag}(u_k(1 - u_k)/2) \), and the matrix \( \mathbf{D} \) takes the form

\[
\mathbf{D} = \begin{bmatrix}
0 & D_{AB} & \cdots & D_{AK} \\
D_{BA} & 0 & \cdots & D_{BK} \\
\vdots & \vdots & \ddots & \vdots \\
D_{KA} & D_{KB} & \cdots & 0
\end{bmatrix}
\]

The matrix \( \mathbf{A} \) is as defined before. The null hypothesis \( H_0 \) implies panmixia, i.e., it assumes that \( \mathbf{A} = \mathbf{I}, \mathbf{D} = \mathbf{0} \). The hypothesis \( H_1 \) allows for gametic disequilibrium (\( \mathbf{D} \neq \mathbf{0} \)) but assumes random union of the disequilibrated gametes (\( \mathbf{A} = \mathbf{I} \)). The hypothesis \( H_2 \), the most general alternative, allows for both disequilibrium (\( \mathbf{D} \neq \mathbf{0} \)) and nonrandom union of gametes (\( \mathbf{A} \neq \mathbf{I} \)).

The test criteria: When applied to the multivariate normal distribution (3), maximum likelihood procedures yield the following estimates of the covariance matrix \( \Sigma \) under the three hypotheses.

\[
H_0: \hat{\Sigma} = \hat{\Gamma} = \text{diag}(\bar{p}_k(1 - \bar{p}_k)/2) \\
H_1: \hat{\Sigma} = \hat{\mathbf{W}} = \hat{\Gamma}^{1/2}\hat{\mathbf{F}}^{1/2} \\
H_2: \hat{\Sigma} = \hat{\mathbf{S}} = \hat{\mathbf{A}}'\hat{\mathbf{W}}\hat{\mathbf{A}}
\]

where \( \hat{\mathbf{S}} \), the observed covariance matrix, is

\[
\hat{\mathbf{S}} = \frac{1}{N} \sum_{j=1}^{N} (\mathbf{Y}_j - \hat{\mathbf{U}})(\mathbf{Y}_j - \hat{\mathbf{U}})'/(N - 1)
\]

with \( N \) the number of individuals sampled and \( \mathbf{R} = \{r_{kl}\} \) the correlation matrix extracted directly from \( \mathbf{S} = \{s_{kl}\} \)

\[
r_{kl} = \frac{(s_{kl})}{(s_{kk} \cdot s_{ll})^{1/2}}
\]
The maximum likelihood estimate of the mean vector $\mathbf{U}$ is given by $\hat{\mathbf{U}} = \hat{\mathbf{P}}$ under all three hypotheses.

The following partitioned set of likelihood ratio test criteria contains all the useful information on the matrix $\hat{\Sigma}$.

$$\Lambda_{02} = -N \left[ \sum_{k=1}^{K} \log(1 + \hat{\theta}_k) - \log(\det \hat{\mathbf{R}}) - \sum_{k=1}^{K} \hat{\theta}_k \right]$$  \hspace{1cm} (9a)  

$$\Lambda_{01} = N \log(\det \hat{\mathbf{R}})$$  \hspace{1cm} (9b)  

$$\Lambda_{12} = -N \sum_{k=A}^{K} \left[ \log(1 + \hat{\theta}_k) - \hat{\theta}_k \right]$$  \hspace{1cm} (9c)

These three criteria are asymptotically distributed as $\chi^2$ random variables with $K(K + 1)/2$, $K(K - 1)/2$, and $K$ degrees of freedom, respectively. Except for the leading constant $N$, which we elsewhere adjust to improve the approximation to a $\chi^2$ (cf. Smouse and Neel 1977), $\Lambda_0$ is the same test criterion we used to test disequilibria in the Yanomama; that earlier analysis is, thus, a special case of the more general treatment provided here. We should mention in passing that $\Lambda_{01}$ is $\chi^2$ distributed only if $H_1$ is acceptable as an explanation of the data. As it develops, this will frequently be the case. The test criterion $\Lambda_{12}$ is a test of the departure from random union of gametes. Such a partition allows one to separate the question of overdispersion ($\Lambda_{12}$) from the question of independence among traits ($\Lambda_{01}$) and is easily derived from standard likelihood ratio manipulations of the multivariate normal distribution (Anderson 1958).

Although we are capitalizing on multivariate normal theory for our analytic strategy, our emphasis is on providing a convenient reference frame, rather than on developing real precision for the various test criteria. These samples and genetic markers depart from strict normality assumptions in a number of particulars, and although the resulting $\chi^2$ test criteria are reasonably robust to violated assumptions, the reader should view the tests as approximations only. The degree of approximation could be improved by various adjustments, but that would be to "gild the lily." Moreover, it is worth remembering that small departures from panmixia can be significant in a large enough sample, whereas even modest departures may not be in a small sample. We have both situations in the analyses that follow. We shall indicate nominal significance wherever it occurs but shall not make an issue of it. The important aspects of the analysis are the estimates themselves and their comparisons across cultural (and agglomeration) levels. As will become apparent later, the comparative trends tell the story clearly.

The estimates: We have found it useful in earlier papers (Smouse and Neel 1977; Smouse, 1982) to reduce $\det \hat{\mathbf{R}}$ to a single correlation-like number in order to indicate the average magnitude of the disequilibrium between a pair of genetic loci. Our practice has been to represent $\hat{\mathbf{R}}$ by that value ($r_e$), which when placed in each off-diagonal position of $\hat{\mathbf{R}}$, yields the same determinant as does $\hat{\mathbf{R}}$. Thus, this effective correlation (average value) is determined by the test criterion and includes information on both the pattern and magnitude of pairwise disequilibria. This effective correlation coefficient can be computed as
the real positive solution to the equation
\[ \det \hat{\mathbf{R}} = (1 - r_e)^K + Kr_e(1 - r_e)^{K-1} \] (10)
and can be viewed as the average standardized disequilibrium for a pair of loci in the population of interest.

It is also useful to reduce the matrix \( \mathbf{A} = \text{diag}((1 + \theta_k)^{1/2}) \) to summary form. We require some sort of average \( \bar{\theta} \) to represent the whole set of the \( \theta_k \)'s, a general measure of departure from random union of gametes. The estimates of the \( \theta_k \) values are obtained as the solutions

\[ \hat{\theta}_k = \text{the kth diagonal element of } [ \mathbf{W}^{-1/2} \mathbf{\hat{W}}^{-1/2} - I ] = \left( \frac{\hat{\theta}_{kk}}{\mathbf{\hat{W}}_{kk}} - 1 \right) \] (11)

A natural estimate of \( \theta \) is given by

\[ \bar{\theta} = \left[ \frac{\sum_{k=1}^{K} \hat{\theta}_k}{K} \right] = \left[ K^{-1} \text{Tr} (\mathbf{\hat{W}}^{-1/2} \mathbf{\hat{W}}^{-1/2} - I ) \right] \] (12)

As mentioned earlier, \( \hat{\theta}_k \) is equivalent to \( \hat{P}_{sk} \) of Neel and Ward (1972), although neither we nor they attach any inbreeding connotation to it.

**Partitioned analysis:** Similar hypothesis testing and estimation procedures can also be applied to whole tribes (or any other collection of villages), using a multivariate analog of the analysis of variance approach described by Cockermam (1969, 1973) for a single locus. It is possible to partition total departures from panmixia within a tribe into a “within-village” component (already described) and a “between-village” component (Smouse and Neel 1977). We first partition the total covariance matrix \( \mathbf{\hat{S}}_T \) into \( \mathbf{\hat{S}}_W \) and \( \mathbf{\hat{S}}_B \), where \( \mathbf{\hat{S}}_W \) is the pooled within-village matrix and \( \mathbf{\hat{S}}_B \) is the between-village matrix. \( \mathbf{\hat{S}}_W \), which provides a weighted average estimate of the within-village variation, is standardized by \( \bar{P}Q/2 \), where \( \bar{P} \) is the average tribal allele frequency. The \( \bar{\theta} \) and \( r_e \) values for \( \mathbf{\hat{S}}_W \) are obtained as already indicated, as are the test criteria (using \( N - I \) instead of \( N \)). The best estimate of the matrix \( \mathbf{\Sigma}_B \) is obtained via a multivariate analog of a “variance components” extraction and is

\[ \mathbf{\Sigma}_B = \frac{(\mathbf{\hat{S}}_B - \mathbf{\hat{S}}_W)}{N - \sum_{i=1}^{I} \frac{N_i^2}{N}} (I - I) \] (13)

where \( I \) is the number of populations sampled. This matrix, \( \mathbf{\Sigma}_B \), has the same general form as that given under hypothesis \( H_2 \) earlier. If there is no population divergence, then \( \mathbf{\Sigma}_B = 0 \). If there is divergence, then the diagonal elements of \( \mathbf{\Sigma}_B \) take the form \( \{a^2_k\} \), where \( a^2_k \) is the variance of allele frequencies among populations at the \( k \)th locus. From standard single-locus theory, \( \hat{\delta}_k^2 = \hat{\theta}_k \cdot \hat{P}_k(1 - \hat{P}_k) \), where \( \hat{\theta}_k \) is the usual \( FST \) measure, and \( \hat{P}_k \) is the overall average allele frequency in the tribe. Thus, the matrix \( \mathbf{A}' = \mathbf{A} = \text{diag} [\hat{\delta}_k] = \text{diag} [\hat{\theta}_k \hat{P}_k(1 - \hat{P}_k)^{1/2}] \), and \( \mathbf{\Sigma}_B = \tilde{\mathbf{A}}_B \mathbf{W}_B \tilde{\mathbf{A}}_B \). The matrix \( \mathbf{W}_B \) is defined as is \( \mathbf{W} \) in (2), without the multiplier of \( (\% \) and using \( \hat{P}_k \) instead of the values for individual villages. If we then define \( \tilde{\mathbf{A}}_B = \text{diag} (\hat{P}_k(1 - \hat{P}_k)) \), again suppressing the multiplier of \( (\% \), the
\( \hat{\theta}_k \) can be estimated by recourse to
\[
\hat{\theta}_k = k^{th} \text{ diagonal element of } [\hat{\Gamma}_B^{-1/2} \Sigma_B \hat{\Gamma}_B^{-1/2}]
\] (14)
The off-diagonal elements of \( \Sigma_B \) take the form
\[
\text{Cov}(P_k, P_l) = \hat{\rho}_{kl}(\hat{\theta}_k \cdot \hat{\theta}_l)(1 - \hat{P}_k)\hat{P}_l(1 - \hat{P}_l)
\] (15)
where \( \hat{\rho}_{kl} \) is an estimate of correlation of population allele frequencies between loci. Thus, the cross-population disequilibrium between the \( k^{th} \) and \( l^{th} \) loci (sometimes denoted as \( D_{ST} \), by analogy with \( F_{ST} \)) is given by
\[
D_{kl} = k,l^{th} \text{ element of } [\hat{\Gamma}_B^{-1/2} \Sigma_B \hat{\Gamma}_B^{-1/2}]
\] (16)
This ensures that \( \hat{\rho}_{kl} \) is the \((k,l)\)th element of \( \hat{\mathbf{R}}_B \), the correlation matrix derived from the covariance matrix \( \Sigma_B \) by the transformation
\[
\hat{\mathbf{R}}_B = \hat{A}_B^T \Sigma_B \hat{A}_B^T
\] (17)
The usual method of testing the hypothesis that the matrix \( \Sigma_B \) is zero (homo-
geneity of allele frequencies across populations) is to construct the likelihood ratio
\[
\lambda_{02} = \frac{\text{det}[(N - I) \cdot \hat{S}_W]}{\text{det}[(N - 1) \cdot \hat{S}_T]}
\] (18)
and then convert to \( \Lambda_{02} = -M \log \lambda_{02} \), where \( M = \left( N - 1 - \frac{K + I}{2} \right) \). The criterion \( \Lambda_{02} \) is asymptotically distributed as a \( \chi^2 \) variable with \( K(I - 1) \) degrees of freedom (Anderson 1958). This Wilks test is not particularly well designed for a convenient partition into separate tests of \( \hat{\theta} \) and \( r_e \), although a series of conditional tests could be constructed to allow for the redundancies implicit in the covariances of \( \Sigma_B \) (cf. Rao 1965, p. 467). We shall simply report the overall test (\( \Lambda_{02} \)) of departures from allele frequency homogeneity across populations and the corresponding \( \hat{\theta} \) values.

RESULTS

Nonrandom mating: The values of \( \hat{\theta} \) and the associated test criteria (\( \Lambda_{12} \)) are presented in Table 2 for all 40 villages, along with the degrees of freedom for each test. In only a single case (village 10A of the Makiritare) is the deviation from random union of gametes \( (\hat{\theta} = 0) \) significant. This particular village has had a very checkered genetic history, having experienced several recent fission and fusion events over a short period (Chagnon et al. 1970; Ward and Neel 1970; Smouse and Ward 1978; J. C. Long and P. E. Smouse, unpublished results); its large excess of homozygotes \( (\hat{\theta} = 0.221) \) probably reflects a strong Wahlund effect (Nei and Li 1973; Smitheock 1975). On the other hand, considering that there were 40 villages examined, perhaps even this single failure of the null hypothesis reflects random sampling and should not be taken too seriously. This general
### TABLE 2

Effective correlation measures ($r_e$) of departures from gametic equilibrium and average measures ($\bar{\theta}$) of departure from random union of gametes for village gene pools in four Amerindian tribal groups, along with respective $\chi^2$ test criteria ($\Lambda_01$ and $\Lambda_{12}$)

<table>
<thead>
<tr>
<th>Tribe and village</th>
<th>Estimated village size</th>
<th>Sample size (N)</th>
<th>Gametic disequilibrium</th>
<th>Nonrandom union of gametes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$r_e$</td>
<td>$\Lambda_{01}$</td>
</tr>
<tr>
<td>Yanomam</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>03KP</td>
<td>103</td>
<td>71</td>
<td>0.120</td>
<td>8.45*</td>
</tr>
<tr>
<td>03LMN</td>
<td>89</td>
<td>58</td>
<td>0.178</td>
<td>14.33</td>
</tr>
<tr>
<td>03Q</td>
<td>43</td>
<td>30</td>
<td>0.197</td>
<td>8.93</td>
</tr>
<tr>
<td>03R</td>
<td>76</td>
<td>41</td>
<td>0.195</td>
<td>11.91</td>
</tr>
<tr>
<td>03T</td>
<td>56</td>
<td>30</td>
<td>0.188</td>
<td>8.14</td>
</tr>
<tr>
<td>03W</td>
<td>83</td>
<td>64</td>
<td>0.146</td>
<td>11.02</td>
</tr>
<tr>
<td>08XY</td>
<td>156</td>
<td>120</td>
<td>0.207</td>
<td>39.96*</td>
</tr>
<tr>
<td>11ABC</td>
<td>208</td>
<td>147</td>
<td>0.051</td>
<td>3.48</td>
</tr>
<tr>
<td>11S</td>
<td>50</td>
<td>39</td>
<td>0.190</td>
<td>10.87</td>
</tr>
<tr>
<td>11V</td>
<td>11</td>
<td>27</td>
<td>0.325</td>
<td>19.91*</td>
</tr>
<tr>
<td>11X</td>
<td>40</td>
<td>43</td>
<td>0.166</td>
<td>9.34</td>
</tr>
<tr>
<td>15H</td>
<td>120</td>
<td>41</td>
<td>0.241</td>
<td>17.50</td>
</tr>
<tr>
<td>Makiritare</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10A</td>
<td>90</td>
<td>64</td>
<td>0.131</td>
<td>8.96</td>
</tr>
<tr>
<td>10BD</td>
<td>176</td>
<td>151</td>
<td>0.116</td>
<td>17.01</td>
</tr>
<tr>
<td>10C</td>
<td>70</td>
<td>43</td>
<td>0.229</td>
<td>16.79</td>
</tr>
<tr>
<td>10E</td>
<td>82</td>
<td>72</td>
<td>0.183</td>
<td>18.62*</td>
</tr>
<tr>
<td>10F</td>
<td>50</td>
<td>44</td>
<td>0.279</td>
<td>24.61*</td>
</tr>
<tr>
<td>10G</td>
<td>110</td>
<td>71</td>
<td>0.244</td>
<td>31.18*</td>
</tr>
<tr>
<td>10HI</td>
<td>130</td>
<td>74</td>
<td>0.146</td>
<td>12.72</td>
</tr>
<tr>
<td>10T</td>
<td>49</td>
<td>36</td>
<td>0.265</td>
<td>18.37*</td>
</tr>
<tr>
<td>10U</td>
<td>55</td>
<td>41</td>
<td>0.290</td>
<td>24.64*</td>
</tr>
<tr>
<td>10V</td>
<td>39</td>
<td>29</td>
<td>0.271</td>
<td>15.37</td>
</tr>
<tr>
<td>10W</td>
<td>31</td>
<td>23</td>
<td>0.296</td>
<td>14.36</td>
</tr>
<tr>
<td>Wapishana</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27A</td>
<td>109</td>
<td>50</td>
<td>0.298</td>
<td>31.51*</td>
</tr>
<tr>
<td>27B</td>
<td>112</td>
<td>47</td>
<td>0.102</td>
<td>4.13</td>
</tr>
<tr>
<td>27D</td>
<td>72</td>
<td>26</td>
<td>0.308</td>
<td>17.46</td>
</tr>
<tr>
<td>27E</td>
<td>123</td>
<td>66</td>
<td>0.304</td>
<td>43.25*</td>
</tr>
<tr>
<td>27F</td>
<td>56</td>
<td>29</td>
<td>0.278</td>
<td>16.15</td>
</tr>
<tr>
<td>27G</td>
<td>102</td>
<td>42</td>
<td>0.210</td>
<td>14.00</td>
</tr>
<tr>
<td>27H</td>
<td>74</td>
<td>31</td>
<td>0.341</td>
<td>25.11*</td>
</tr>
<tr>
<td>27K</td>
<td>149</td>
<td>61</td>
<td>0.137</td>
<td>9.32</td>
</tr>
<tr>
<td>27L</td>
<td>168</td>
<td>91</td>
<td>0.110</td>
<td>9.29</td>
</tr>
<tr>
<td>27M</td>
<td>93</td>
<td>47</td>
<td>0.212</td>
<td>15.95</td>
</tr>
<tr>
<td>Ticuna</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>37A-E</td>
<td>1250</td>
<td>343</td>
<td>0.067</td>
<td>13.67</td>
</tr>
<tr>
<td>37F</td>
<td>275</td>
<td>86</td>
<td>0.170</td>
<td>19.46*</td>
</tr>
<tr>
<td>37GH</td>
<td>360</td>
<td>120</td>
<td>0.175</td>
<td>28.52*</td>
</tr>
<tr>
<td>37J-N</td>
<td>700</td>
<td>294</td>
<td>0.072</td>
<td>13.30</td>
</tr>
<tr>
<td>37PR</td>
<td>700</td>
<td>141</td>
<td>0.094</td>
<td>10.77</td>
</tr>
<tr>
<td>37T-Y</td>
<td>900</td>
<td>369</td>
<td>0.094</td>
<td>28.00*</td>
</tr>
<tr>
<td>43A-D</td>
<td>2000</td>
<td>253</td>
<td>0.108</td>
<td>24.68*</td>
</tr>
</tbody>
</table>

* d.f. = 10; * d.f. = 5. * Significant at $\alpha = 0.05$ level.

142
failure to demonstrate nonrandom union of gametes is entirely in keeping with
the earlier finding by Neel and Ward (1972) that locus-specific $F_{IS}$ values were
nonsignificantly different from zero in a set of Yanomama, Makiritare and
Xavante villages. Both gene flow and drift create nonzero $F_{IS}$ values (cf. Smouse
1982), but the $\chi^2$ test of the departure of these coefficients from zero has very
little statistical power (Lewontin and Cockerham 1959; Ward and Sing 1970;
Chakraborty and Rao 1972; Haber 1980). Moreover, mating within a village is
sufficiently random with respect to genotype that most villages at any particular
moment will be fairly close to equilibrium. As a consequence, $\bar{\theta}$ is a poor gauge
of the genetic consequences of social and demographic organization.

One of the more intriguing observations of Neel and Ward (1972), however,
was that the $F_{IS}$ values were quite frequently negative (excess of heterozygotes)
in the Yanomama, in spite of an apparent excess of inbreeding over random
expectation. If $\theta = 0$ on the average (a hypothesis we cannot falsify statistically
in the individual cases), then one might expect to find that the $\theta_k$ estimates are
as often negative as positive. Of a total of 200 single-locus $\theta_k$ estimates for the
40 villages examined, however, 119 are negative and 81 are positive. Neel and
Ward (1972) comment that excesses of heterozygotes are to be expected not
only with heterozygote advantage, small deme size, or differential fertility, but
also when allele frequencies for a particular locus are different in the two sexes
of parent, a theoretical point originally made by Robertson (1965). Since
approximately 17% of Yanomama marriages are village exogamous (MacCluer,
Neel and Chagnon 1971), and since allele frequencies almost always differ
among these small villages (cf. Smouse, Spielman and Park 1982), this sex
differential in frequencies among mates is virtually guaranteed. It may be that
the other tribal groups, with less pronounced sexual asymmetry of migration
rates, show a more balanced set of $\theta_k$ estimates or perhaps even a slight excess
of positive values. A complete enumeration yields the following results.

<table>
<thead>
<tr>
<th>Tribe</th>
<th>$\text{No. } (\hat{\theta}_k &gt; 0)$</th>
<th>$\text{No. } (\hat{\theta}_k &lt; 0)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yanomama</td>
<td>21</td>
<td>39</td>
</tr>
<tr>
<td>Makiritare</td>
<td>21</td>
<td>34</td>
</tr>
<tr>
<td>Wapishana</td>
<td>20</td>
<td>30</td>
</tr>
<tr>
<td>Ticuna</td>
<td>19</td>
<td>16</td>
</tr>
</tbody>
</table>

The Makiritare and Wapishana also show an excess of negative values, whereas
the Ticuna show a deficit of negative values. More important is the observation
that the proportion of negative values appears to decrease as the level of
acculturation increases (Yanomama $\rightarrow$ Makiritare $\rightarrow$ Wapishana $\rightarrow$ Ticuna).

There is, however, one additional possibility that warrants comment. Majum-
der and Chakraborty (1981) have shown that, in small samples drawn from
equilibrium Hardy-Weinberg gene pools, the probability of drawing an ex-
cess of heterozygotes is generally greater than one-half because of multi-
nominal sampling considerations. When population allele frequencies depart
substantially from $P_k = \frac{1}{2}$, the probability of an excess in the sample
($\hat{\theta}_k < 0$) is substantially greater than one-half. The Yanomama villages have
allele frequencies that are generally farthest from $P_k = \frac{1}{2}$, and this appears to account for much of the difference. A detailed examination of the pattern of positive and negative $\theta_k$ estimates indicates that tribal membership (and its sociocultural consequences) are largely irrelevant, except insofar as they determine allele frequency dispersion and available sample sizes. Two variables, both anticipated by Majumder and Chakraborty (1981), are important in determining the degree of sign asymmetry for the $\theta_k$ estimates: sample size ($n$) and the degree of departure ($\delta$) of a particular allele frequency from ($\frac{1}{2}$). Summarizing across tribes, we obtain the following results, listed as the numbers of (+) and (−) $\theta_k$ estimates.

<table>
<thead>
<tr>
<th>$0 \leq n &lt; 50$</th>
<th>$50 \leq n &lt; 100$</th>
<th>$100 \leq n &lt; 400$</th>
<th>All ($n$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(+) (−)</td>
<td>(+) (−)</td>
<td>(+) (−)</td>
<td></td>
</tr>
<tr>
<td>0 &lt; $\delta$ &lt; 0.2</td>
<td>12:22</td>
<td>10:11</td>
<td>6:5</td>
</tr>
<tr>
<td>0.2 &lt; $\delta$ &lt; 0.4</td>
<td>19:26</td>
<td>11:22</td>
<td>12:12</td>
</tr>
<tr>
<td>0.4 &lt; $\delta$ &lt; 0.5</td>
<td>3:13</td>
<td>2:4</td>
<td>6:4</td>
</tr>
<tr>
<td>All ($\delta$)</td>
<td>34:61</td>
<td>23:37</td>
<td>24:21</td>
</tr>
</tbody>
</table>

The detailed pattern of values within the body of this array is a bit erratic because of the small numbers involved, but an examination of marginal totals yields the predicted results. The tally of $\theta_k$ estimates is 42.4%+, 41.2%+ and 34.4%+ for $0 < \delta < 0.2$, $0.2 < \delta < 0.4$, and $0.4 < \delta < 0.5$, respectively. A similar tally yields 34.8%+, 38.3%+ and 53.3%+ for $0 \leq n < 50$, $50 \leq n < 100$, and $100 \leq n < 400$, respectively. In light of these sampling considerations, we are inclined to view the distribution of signs for these small, nonsignificant departures from single-locus panmixia as due primarily to sampling artifacts. They are probably of no biological importance.

Gametic disequilibrium: The estimated $r_e$ values and the associated test criteria ($A_{01}$) are also listed for all 40 villages in Table 2. Of the 40 values listed, 14 are significantly different from zero. As was the case for the earlier Yano-mama analyses (Smouse and Neel 1977), the disruptive influences of random drift and village exogamy are sufficient to maintain substantial levels of gametic disequilibrium within village gene pools. The comparison of tribal groups in different stages of acculturation, however, yields an interesting result. The magnitudes of the $r_e$ values appear to depend primarily on village size, irrespective of cultural detail. The results are presented graphically in Figure 1, where $r_e$ is plotted against the log of village size. The trend is very clear: the larger the village, the smaller the disequilibrium. There are two features of the demographic organization of village gene pools that may explain these results. First, larger villages experience less genetic drift and, thus, less divergence between villages in allelic frequencies; with small divergence, very little disequilibrium can be generated by gene flow between villages. Second, small villages tend to be more exogamous, probably because of the difficulty of finding a suitable mate (proper age and kinship relationship) in a small village (cf. MacCluer, Neel and Chagnon 1971). For any pair of villages, the contribution of migration
to disequilibrium is proportional to \( m(1 - m) \), where \( m \) is the exogamy rate (usually less than 0.50). Thus, large \( m \) implies large disequilibrium, everything else being equal.

The Ticuna are particularly interesting in this regard. Although this tribe has the largest villages in the study, such large villages are of relatively recent origin. The agglomerative phase of Ticuna social organization dates back no more than two generations (Nimuendajú 1952), and migration between these sizeable towns has been considerable. Although the disequilibria are significant in four of seven villages (because of large sample sizes), they are not large (\( r_e < 0.2 \) in all villages). A priori we would have expected larger disequilibria, since there appears to have been insufficient time to establish equilibrium. Two factors may be involved in this unexpectedly rapid approach to panmixia. First, the disequilibrium within a village is a weighted average of that within each of the donor villages one generation earlier, plus that produced by migration. The disequilibrium for any specific pair of loci shows no particular consistency of sign (+ or −) from village to village, however, and tends to average out very close to zero for a whole tribe (Smouse and Neel 1977). In this situation, wholesale mixing should yield small disequilibria. Second, the Ticuna settlements are now so large that further genetic drift can be largely ignored, and whereas genetic distances between the original villages may well have been
Effective correlation measures ($r_e$) of departures from gametic equilibrium and average measures ($\theta$) of departures from random union of gametes, extracted from the within-population ($\Sigma_w$), between-population ($\Sigma_b$) and total ($\Sigma_t = \Sigma_w + \Sigma_b$) covariance matrices of four Amerindian tribal groups, along with approximate $\chi^2$-test criteria

<table>
<thead>
<tr>
<th>Matrix used for analysis</th>
<th>Yanomama</th>
<th>Makiritare</th>
<th>Wapishana</th>
<th>Ticuna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tribal group</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within villages</td>
<td>$[\Sigma_w]$</td>
<td>$(N-1) = 699$</td>
<td>$(N-1) = 637$</td>
<td>$(N-1) = 480$</td>
</tr>
<tr>
<td>$r_e$</td>
<td>0.0530</td>
<td>0.0580</td>
<td>0.0560</td>
<td>0.0250</td>
</tr>
<tr>
<td>$\Lambda_02^a$</td>
<td>17.90</td>
<td>19.60*</td>
<td>13.75</td>
<td>9.84</td>
</tr>
<tr>
<td>$\theta_{IS}$</td>
<td>-0.0897</td>
<td>-0.0683</td>
<td>-0.0487</td>
<td>-0.0147</td>
</tr>
<tr>
<td>$\Lambda_{IS}^b$</td>
<td>14.97*</td>
<td>7.60</td>
<td>2.94</td>
<td>8.77</td>
</tr>
<tr>
<td>Between villages</td>
<td>$[\Sigma_b]$</td>
<td>$(l-1) = 11$</td>
<td>$(l-1) = 10$</td>
<td>$(l-1) = 9$</td>
</tr>
<tr>
<td>$\theta_{ST}$</td>
<td>0.0630</td>
<td>0.0482</td>
<td>0.0323</td>
<td>0.0133</td>
</tr>
<tr>
<td>$\Lambda_02$</td>
<td>428.47*</td>
<td>305.52*</td>
<td>179.97*</td>
<td>204.32*</td>
</tr>
<tr>
<td>d.f.</td>
<td>55</td>
<td>50</td>
<td>45</td>
<td>30</td>
</tr>
<tr>
<td>Between individuals</td>
<td>$[\Sigma_T]$</td>
<td>$(N-1) = 710$</td>
<td>$(N-1) = 647$</td>
<td>$(N-1) = 489$</td>
</tr>
<tr>
<td>$r_e$</td>
<td>0.0940</td>
<td>0.0840</td>
<td>0.0720</td>
<td>0.0330</td>
</tr>
<tr>
<td>$\theta_{IT}$</td>
<td>0.0364</td>
<td>0.0280</td>
<td>0.0160</td>
<td>0.0119</td>
</tr>
</tbody>
</table>

*a* d.f. = 10.

*b* d.f. = 5.

* Significant at $\alpha = 0.05$ level.

large, those between the extant towns are small (Neel et al. 1980). If the towns differ very little in allele frequencies, gene flow produces minimal new disequilibria.

Cross-population comparisons: The failure of tribal panmixia is also evident in the packaging of genetic variation within and between villages. The analyses of the matrices $\Sigma_w$ and $\Sigma_b$ are presented in Table 3 for each of the tribes examined. The $r_e$ estimates from $\Sigma_w$ are smaller than those for individual villages in all four tribes (Table 2). As mentioned before, this is an indication that the pattern and direction of disequilibria vary randomly from village to village, averaging near zero for any pair of unlinked loci (Smouse and Neel 1977). The Ticuna value is less than half that of the other three tribes, as might have been anticipated on the basis of village size differences. The $\theta$ values are also close to zero, averaged over villages, and all values are negative. Wright (1951, 1965) has shown that $F_{IS}$ is given by $F_{IS} = (F_{IT} - F_{ST})/(1 - F_{ST})$ and has pointed out that, if $F_{ST} > F_{IT}$, then $F_{IS}$ will be negative, as it is here for all four tribes. The Yanomama value is a marginally significant departure from zero, but the other values are nonsignificant. More important is the observation that there is a progression from the Yanomama to the Ticuna, with the latter showing almost no average departure from panmixia within villages.

The between-village results are also dramatic and differ rather markedly from tribe to tribe. It is evident from Table 3 that $\theta$ from $\Sigma_b$ decreases toward zero as one moves from the small villages of the Yanomama to the large villages of the
Ticuna, with the Makiritare and Wapishana giving intermediate results. The test criteria are all significant, but tribal sample sizes are large enough that even small departures from homogeneity are significant. These results are entirely in keeping with the predicted consequences of agglomeration, and the pattern is at least as striking as that presented by the within-village results.

Finally, to gauge the departures from tribal panmixia, irrespective of village designation, we present in Table 3 both the $\bar{\theta}$ and $r_e$ values extracted from the matrix $\Sigma_T = \Sigma_B + \Sigma_W$. The $\theta$ term is now equivalent to $F_{TT}$ in the usual treatment, whereas $r_e$ now represents the correlation between the genotypes of an average pair of unlinked loci in an individual drawn at random from the tribe. Again, both $\bar{\theta}$ and $r_e$ decrease dramatically as one moves from the Yanomama to the Ticuna, consistent with the expected consequences of agglomeration.

To place these trends into larger perspective, we find it useful to compare our results with those of SINNOCK and SING (1972a,b), who reported two-locus departures from panmixia in the community of Tecumseh, Michigan. Tecumseh contains elements from several European populations, rather thoroughly mixed over a longer period of time. As a population, it is considerably closer to the panmictic "regional gene pool" we alluded to earlier than are even the Ticuna. The data provided by SINNOCK and SING (1972a,b) are best compared with those we have derived from $\Sigma_T$ in Table 3. Using their data for the Mn, RhE, Hp and Gc loci, we obtain $\bar{\theta} = -0.0015$ and $r_e = 0.0190$; with a population size of $N \sim 10,500$, these results simply extend the sequence beyond the Ticuna in the predicted direction. The remaining small departures from panmixia in Tecumseh can plausibly be traced to the diverse ethnic ancestry of that community, but it is not really feasible to partition the gene pool into meaningful ethnic subdivisions at this late date. It appears that the convergence of the gene pool toward panmixia is an exponential decay process, measured either against population size or time since agglomeration. Initial convergence is very rapid, as in the Ticuna, but the final approach to equilibrium is slow.

DISCUSSION

The exact theoretical details of the dynamics of departures from multiple-locus panmixia, under the countervailing influences of drift and gene flow, have never been completely resolved. HARpending and WARD (1982) and J. W. WOOD (unpublished results) have shown that a quasistable set of single-locus $F_{ST}$ values will result from the countervailing processes of genetic drift and migration. NEI and LI (1973) and FELDMAN and CHRISTIANSEN (1975) have described the dynamics of the gametic disequilibria under pure migration, but with no countervailing pressures, the disequilibria all converge to zero. It has never been formally proven that the addition of drift to the generalized migration model will lead to a quasistable array of nonzero disequilibria as well, but OHTA (1982) has demonstrated such an equilibrium for the classical island model of migration. A simple line of argument can be used to make the existence of such an array plausible in general. As already mentioned, under migration and drift, we can expect semipermanent differences between allele frequencies in different villages. Such allele frequency differences alone are sufficient to generate
gametic disequilibria (SMOUSE 1982). The departures from panmixia that we have described should thus characterize most subdivided gene pools.

The picture we are painting here is that of Homo sapiens at the small group level of social organization. We have shown that the agglomeration that often accompanies acculturation rapidly converts a subdivided population to the nearly panmictic state of modern cosmopolitan populations. It seems fairly obvious, however, that most of human evolution and human radiation occurred under small group conditions. We have argued elsewhere that the most prominent feature of Amerindian tribal organization in the lowlands is the small effective size of the village gene pool (cf. NEEL 1978b; SMOUSE 1982), and that the principal short-term influence on the gene pool is random drift. From the results presented here, it is clear that this observation is valid for any tribe that still manifests small group social organization. If one measures genotype frequencies relative to tribal average allele frequencies, departures from panmixia are substantial.

To see what this means for evolution, imagine that the selective pressures imposed by ecological factors would (for a tribally panmictic population) result in a set of polymorphic allele frequencies at some particular set of loci. The optimal distribution of genotypes would then be a panmictic array determined by the optimal allele frequencies at the various loci. (Recall that we are describing unlinked loci for which epistatically produced disequilibria are unlikely to be maintained.) We are, of course, in no position to prove that any of the loci under current examination (primarily blood group antigen and serum protein loci) are themselves being maintained in a polymorphic state by natural selection, but there are undoubtedly other loci that are so maintained, and the stochastic aspect of their dynamics would be the same as those of the marker loci we have examined here. Moreover, it should not have escaped the readers’ notice that these polymorphic blood groups and serum proteins are the same ones showing persistent polymorphism in almost every human population. These native Amerindians are relatively monomorphic for the sorts of loci known to segregate elsewhere (NEEL 1978a), suggesting that random fixation has been a prominent feature of their gene pool dynamics. Against this backdrop, the stubborn persistence of these traditional polymorphisms is all the more remarkable, and perhaps we should not invoke neutrality with any degree of confidence.

Given the highly subdivided nature of tribal gene pools, however, any accurate and precise tracking of an adaptive optimum would not be possible. In some aggregate sense, the tribal gene pool has average allele frequencies that are reasonably close to those implied by the optimum point on the adaptive landscape. The individual villages, however, depart so far from this optimum point that the optimum is virtually never occupied. Moreover, the genetic organization of the tribe is highly erratic over time and space, and villages move unpredictably from one position to another on the adaptive landscape. Under such circumstances, it is difficult to see how the aggregate population could respond precisely to adaptive cues. Tracking an adaptive optimum becomes a trial and error process, in which the average point of impact is the center of the target but the target itself is seldom (if ever) hit.
This inability of highly subdivided populations to hit the adaptive target might have its evolutionary compensations, however. Instead of a single adaptive peak, imagine that there are several quite different optima in different regions of the available genetic space, producing a hill-and-valley adaptive topology. A large panmictic population, whose dynamics were dominated by deterministic (selective) forces, would inevitably climb whatever adaptive slope it was already on and would converge in due course on the center of the target (the local optimum). Such a population, however, would be largely precluded from scaling any other adaptive peak separated by a valley; there might be a higher hill than that currently occupied, but there would be no way to get there from the present position. A highly subdivided population with the propensity to jump randomly from one point on the landscape to another would sample a much larger fraction of the adaptive landscape and would tend to climb several adaptive peaks simultaneously. Although never actually capturing and holding the highest adaptive peak, a subdivided population would almost always find it and, given some migration between subdivisions, surround it. In a situation in which the environment changes over space and time, a subdivided population should generally track faster and adapt more flexibly than a large panmictic unit. This is the shifting-balance scenario originally presented by Wright (1931, 1970, 1982), and the population structure of lowland tribal Amerindians is precisely that under which such a scenario would be operative. The ability of large modern aggregates to capture and hold the local adaptive optimum is quite good, but they are largely restricted to a single adaptive peak. Evolutionary accuracy and precision is improved at the expense of flexibility, so that evolutionary progress of modern conglomerate human populations is more predictable (in a deterministic sense) but also more conservative than that of our tribal antecedents. Otherwise stated, the stochastic process creates some problems for a population "attempting to climb" a particular adaptive peak, but it also creates some unusual "opportunities."

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DEPARTURES FROM PANMIXIA 151


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