

## The genetic structure of a tribal population, the Yanomama Indians

### 1. Introduction

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To the extent that a key issue can ever be identified in biology, understanding the significance of the large amount of genetic variation encountered in all properly studied outbreeding plant and animal species is the key issue in population genetics today. A meaningful discussion of this issue is seriously hampered by lack of data on the breeding structure of natural populations. Human populations offer unusual advantages for the study of population structure. Ancestry and recent patterns of migration of individuals and groups can be determined with a precision not possible for other 'wild' populations, as can individual reproductive performances. History and archaeology supply additional data on population movements in the past also usually not available for other types of organisms.

While data on all types of human populations are greatly to be desired, data on the surviving relatively unacculturated, tribal-type populations are especially critical. The parameters of these populations come closest to reflecting the circumstances under which human evolution occurred and under which the vast amount of variability now known to be present in human populations arose. Such populations will not long be available for study.

Guided by these and other considerations, in 1961 we initiated a major programme directed towards the American Indian (Neel & Salzano, 1964). With particular respect to the matter of the population structure of a relatively unacculturated group, the Xavante Indians of Brazil were chosen as the objects of a pilot study (cf. Neel *et al.* 1964). Even while this study was in progress, an intensive effort was being made to locate a larger and less acculturated Indian tribe, but one whose study did not present insuperable logistic problems. In this effort we were greatly aided by the expert knowledge of Professors Francisco Salzano and Miguel Layrisse.

The choice finally settled on the Yanomama Indians of northern Brazil and southern Venezuela, a tribe of some 10,000 individuals first touched by missionary activity in 1950. Their approximate distribution is between latitudes 1 and 5° N and longitudes 62 and 65° 30' W. Although several expeditions or individual explorers had traversed portions of the territory they occupy prior to 1950 (Schomburgk in 1837, Koch-Grünberg in 1911, Rice in 1919–20, Salathé in 1930), as far as is known the contacts when not actually hostile (Rice, 1921) had been fleeting. Even at the height of the natural rubber boom, tappers do not seem to have penetrated this area. At present there are about a dozen mission stations within the area occupied by the Yanomama; the clearing of air-strips at seven of the stations during the past decade was an important logistic consideration in the choice of the tribe. However, despite this intrusion of missionaries, to whose spiritual ministrations the Yanomama have been unusually resistant, we estimate that perhaps a third of the estimated 100–125 Yanomama villages are yet to be visited by a white man. A good index

of the tribe's relative isolation is the fact that at the time of our first contacts they were, with the exception of two villages, a 'virgin-soil' population for measles (Neel *et al.* 1970).

Relatively little has been written concerning Yanomama culture thus far, the chief contributions being those of Becher (1960), Zerries (1964), Barandiarán (1965, 1967), Chagnon (1968*a, b*) and Biocca (1970). Materially it is a very simple culture, whose economy is based on slash-and-burn agriculture and hunting-and-gathering. In the present context it is important to recognize the evidence that the tribe has expanded to the south and west within the past century (Chagnon, 1968*a*). To the extent that an expanding tribe possesses attributes not found in a stable tribe, this must be borne in mind in interpreting the generality of the findings to be presented. On the other hand, such periods of expansion must have occurred frequently in human history.

Despite the relatively pristine nature of the group, there are at least four types of evidence that indicate substantial departures from the pre-Columbian state (cf. Neel, 1971):

(1) Even the most remote villages contacted during the past 20 years by various individuals have had a few battered machetes or pieces thereof, acquired through native trade channels. Although no Yanomama village has yet been encountered using stone axes for agricultural purposes, such axes are very commonly found throughout the Yanomama distribution, and presumably were previously employed to gird trees, before firing them. The machete is enormously more efficient for this purpose.

(2) The cooking banana (*Musa paradisiaca*), generally regarded as a post-Columbian introduction to the New World, is now the principal source of calories in their slash-and-burn agriculture. The acquisition of the machete and the cooking banana must have greatly altered their food base from that obtaining in pre-Columbian times.

(3) Disease patterns are changing. The following are a few examples. On the basis of both clinical and serological evidence, malaria and yellow fever, both probably introductions from the Old World, are now common among the Yanomama. An epidemic of measles, perhaps the first, swept through a large portion of the tribal area in 1968 (Neel *et al.* 1970). The Yanomama have been a forest rather than a river people, but now many villages are moving to the river's edge, for better access to trade goods. One obvious consequence is greater exposure to such insects as the biting midges, with, in children especially, secondary infections of scalp and skin. Dental caries are common in children in those villages where contacts with missionaries go back as long as ten years. In addition, interesting and subtle changes are occurring in the metabolism of iodine (Rivière *et al.* 1968) and, possibly, other minerals.

(4) In the four Yanomama villages chosen for intensive demographic studies, there are fewer persons with an estimated age of 1-14 years than 15-30 (Neel & Chagnon, 1968). The deficiency is especially marked in the interval 10-14, suggesting exposure to some epidemic disease(s) with especially high mortality in infancy some ten years ago. Although the postulated disease(s) may have been autochthonous in origin, an introduction from outside cannot be excluded.

The departures from the pre-Columbian population dynamics which these and other changes may have occasioned are by no means clear. As noted earlier, the limited data suggest that within this century the tribe has expanded to the south and west. This could be a result of an improved food base influencing reproductive indices, the cooking banana playing the role here that the potato may have played in the spectacular population increase in Europe of the mid-eighteenth century (Langer, 1963). We do not present these Indians as accurately reflecting the pre-

Columbian state – only as one of the better approximations thereto remaining in South America today. By the same token, it is clear they depart greatly from true hunter-gatherers. Unfortunately, the remaining groups of the latter are either so disturbed, so few in their numbers, or so inaccessible, that their usefulness and validity in the development and testing of genetic hypotheses seem dubious.

Thus far, we have employed the term ‘tribe’ as if it were a standard categorization. In fact, there is continuing debate concerning the precise connotations of the term. Three facts justify our subsequent treatment of the thirty-seven village samples we will describe as having been drawn from a single tribe. (1) As contrasted to their nearest tribal neighbours (Makiritare, Piaroa, Macushi), the Yanomama have a distinctive common culture (cf. Chagnon, 1968*a*). (2) Although there are important dialectical differences from one area of the Yanomama distribution to another, even the most differentiated dialects have approximately 70 % of the content of a standard word list in common. None of these dialects is closely related to any of the languages employed by the surrounding tribes (Migliazza, personal communication). (3) Finally, the various villages appear to be interconnected by a web of migration matrices, usually traversed peacefully. Although in the past there has undoubtedly been inter-tribal ‘migration’ to and from tribes such as the Makiritare and the Máku, this in our opinion was probably more limited than the inter-village migration and more often accompanied by a state of overt hostility than intra-tribal migration (cf. Chagnon *et al.* 1970). Thus, to the cultural considerations that enter into the definition of a tribe we add a genetic, namely a common migration matrix whose boundaries are only occasionally traversed, and then usually by virtue of hostile acts.

Our contacts with the Yanomama were initiated in 1964, when Dr Napoleon Chagnon began his ethnological studies among them. This has been followed by six multidisciplinary expeditions, in 1966, 1967, 1968, 1969, 1970 and 1971. It will be the purpose of this series of papers to summarize the principal findings thus far concerning the population structure of the Yanomama and some of its possible consequences. More specifically, on the basis of phenotype determinations for some twenty-seven different genetic systems, we will first describe the degree of local genetic differentiation encountered in thirty-seven villages. The location of these villages is shown in Ward (1972). Genetic distances and genetic trees (phylogenies) will be derived, and the robustness of these tested by parallel data on the ethnohistory, geographical distribution, physical measurements and linguistic differentiation of the Yanomama. In this connexion, the tribe has been seen as a microcosm in which to attempt to validate and improve distance measurements. The breeding structure and demography will be described, including data on fertility, mortality, infanticide, inbreeding, polygyny, migration matrices and settlement patterns. These data will be applied to an understanding of the observed genetic microdifferentiation, which will be characterized not only by distance functions but also by Wright’s hierarchical  $F$ -statistics and Malecot-type formulations. Some of the implications of this breeding structure will be explored through computer simulation, especially the intensity of inbreeding, the possibilities for genetic drift and the possible stabilizing role of selection. The difference between simulated and observed inbreeding levels and those predicted by departures from Hardy–Weinberg equilibrium will be analysed in series of individuals and of mating types. Data will be presented on consanguinity effects at this cultural level. Evidence will be sought for distortions of genetic ratios and non-random genetic associations (co-adaptation), although the data are so limited that only in association with the data of others is there any hope of demonstrating even rather major selective differentials. In

parallel papers we shall be describing the general health of the Indian and his interaction with local pathogens, as determined by extensive serological and isolation studies.

In short, what is involved is an effort to obtain insights into the genetic structure of human populations during the long period of pre-civilization. In the widest sense, this extends to attempts to visualize the interaction of a constantly changing but structured array of phenotypes with an equally varying but equally structured ecosystem. It has been our hope to develop at this societal level insights denied us in the study of civilized groups both because of the breakdown of the original population structure and a highly disturbed ecosystem.

As the studies have progressed, similar investigations on other primitive or recently primitive peoples have been emerging – for example, those of Cavalli-Sforza and colleagues on African pygmies, Kirk and colleagues on the Australian aborigine, the Harvard group in the Solomon Islands, Laughlin and colleagues among the Eskimo, and the work of numerous investigators in New Guinea. The careful comparison and integration of the results of all these studies will be essential in the definition of common denominators which by their constancy give confidence in their validity.

Those who appreciate the logistic and human problems in investigations of this type will perhaps be more charitable of some of the shortcomings of the data than those who have never worked in an essentially undisturbed tropical rain forest, among a relatively unacculturated and sovereign tribe. The disappointment of arriving at a village site after a wearying passage, only to find it deserted; the joy of unexpectedly encountering the total population of a previously unstudied village, as visitors to another village; the challenge of entry into a village previously visited by only two or three other white men or even none – these are the patterns of the work. Over it all looms the recognition – from encounters on the trail or cheek-by-jowl hammocks in the night of an Indian village – that these people are ourselves, with the objective approaches to measuring our common humanity and its origins only now coming to hand.

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