Further Studies on the Xavante Indians

X. Some Hypotheses-Generalizations Resulting From These Studies

JAMES V. NEEL [1] AND FRANCISCO M. SALZANO [2]

[1]*Department of Human Genetics,*
University of Michigan Medical School,
Ann Arbor 48104.
[2]*Departamento de Genética,*
Instituto de Ciências Naturais,
Universidade Federal do Rio Grande do Sul,
Pôrto Alegre, Brazil.

THE INVESTIGATIONS reported in the preceding seven papers in this series represent an effort to try to begin to understand and quantitate the breeding structure and the important biological determinants in the survival and reproduction of certain primitive peoples, the adjective primitive being employed as a convenient synonym for a nonmaterial culture whose economy is based on hunting and gathering with or without simple agriculture or pastoralism. A further characterization of such cultures has often been that their social organization is based on kinship (clans, moieties, etc.) or kinship-like (age-graded societies, warrior associations) institutions and that their internal affairs are not subject to the control of higher political organizations.

Although the effort to study the genetic structure of primitive man is a sufficient objective of itself, there is the further possibility that the investigation of these more simply structured communities may point the way toward factors of importance in more complex communities, factors which have been obscured by the very complexity of the situation. Profoundly aware though we are of the imperfections in current methodology, we feel the problems cannot wait until these imperfections are resolved—for by then the opportunity to study these problems may be gone. It seems self-evident that much about contemporary man can be truly understood only in the light of his past, and the prospects of reconstructing many aspects of this past are rapidly diminishing. Unfortunately, the data which the biologically-oriented would consider most meaningful simply cannot be abstracted from the voluminous anthropological literature. It was perhaps, at least in part, the realization of this and related points which led Levi-Strauss (1963) to write: "Surprisingly enough, it is at the very moment when anthropology finds itself closer than ever to the long-awaited goal of becoming a true science that the ground seems to fail where it was expected to be the firmest: the facts themselves are lacking."

The program of which these studies form a part is concerned with the

---

Received November 14, 1966.

American Indian and has three overlapping subdivisions (Neel and Salzano, 1964), namely, (1) an effort, primarily utilizing gene frequencies, to understand the nature and tempo of human divergence in the Americas; (2) an effort to define the population structure of the pre-Colombian Indian, and the major biological determinants interacting with that structure; and (3) an effort to define the genetic consequences of the rapid acculturation which many Indian groups have undergone.

In this final paper in the present series, we will concentrate the discussion on point (2) above, leaving items (1) and (3) for future communications. We will attempt to develop, on the basis of the foregoing seven papers, a series of hypotheses-generalizations concerning the Xavante which will shape the course of future work on other groups. Some of these hypotheses-generalizations are major, some are minor; some are relatively new, others well represented in the literature; and finally, some have "strong inference" properties (Platt, 1966), others do not suggest clear-cut alternatives. Relatively little effort will be directed, at this time, towards developing a comprehensive and detailed population model based on the Xavante, on the thesis that this would be premature since other work in progress on the Yanomama of the upper Orinoco region of Venezuela and the Cayapo of the Northern Mato Grosso and Southern Pará regions of Brazil will provide much more information against which both to test the generality of the present observations and to develop one or several specific population structures.

A persistent criticism of studies of this type has been that the surviving primitive groups are all in some way atypical and hence of no real value in providing the desired insights. It seems self-evident that there are few if any groups of this nature uninfluenced by contacts with higher cultures. Such contacts can result either in cultural impoverishment, as when the contact displaces the group into an area which will not readily provide the raw material for former skills, as pottery making, or in cultural "enrichment," as when contact results in firearms which alter traditional ways of hunting. The possibility that certain population parameters may have undergone serious distortions cannot be denied. But to denigrate these studies simply because the Garden of Eden is no longer pristine is surely not the scientific approach. There is a clear challenge to the geneticist to join in the study of these cultures in the greatest depth possible while the opportunity still persists, mindful of the presence of cultural contamination, striving (in the case of the American Indian) to detect post-Colombian influences, and searching among groups for common denominators which by their constancy suggest their primordial nature.

Repeatedly in the foregoing papers, and again in this one, difficulties have been encountered in subjecting alternatives to statistical tests. The statistics of population genetics are with few exceptions either "large sample" statistics or applicable to small samples—such as primitive populations are—only under rather restrictive assumptions. By applying the full battery of genetic observations to as many members of each small village as possible, one accumulates valuable material for the analysis of breeding structure, distortions in genetic ratios, inheritance of new or rare qualitative traits, or estimates of heritability for quantitative traits. However, one encounters problems in attempting to contrast the findings in two villages of one tribe, or even in two tribes. A village study does not entail sampling from a large population, but sampling without replacement from a small population, with the sampling often so complete as to approach a total enumeration. In the past, investigators have attempted to meet this problem by using for certain calculations and contrasts "apparently unrelated persons." Unfortunately, at the cultural level represented in studies of this type, genealogies are usually so poor that while this device might satisfy the investigator's conscience, it does not solve the problem. This is not only a problem in the study of American Indians—one wonders, for instance, about the independence of the observations on which are based the χ^2 values in the recent studies of Nichols *et al.* (1965) on Central Australian aborigines or of Nijenhuis *et al.* (1966) and Giles *et al.* (1966) on the natives of New Guinea.

We turn now to a consideration of some of the salient points emerging from the present studies. When in this consideration we use the term *tribe*, it will be in the conventional and acknowledgedly somewhat unsatisfactory sense of a group sharing a common language and customs—no better term has yet been evolved.

A. THE GENETIC STRUCTURE OF THE XAVANTE IS A FISSION-FUSION TYPE WHICH DIFFERS IN IMPORTANT RESPECTS FROM THE VARIOUS POPULATION MODELS PROPOSED THUS FAR.

At any specific moment in time, a Xavante village may appear highly endogamous. Periodically, however, as the tensions inherent in the social relationships of strong males accumulate, the village, already split into two or more factions, undergoes a physical fission. The smaller product of this fission, numbering some 40–60 persons, may take any one of four courses, namely, join another village (often at a considerable distance), form a new village, rejoin the original village after a period of "cooling off," or, if it wanders so far from other villages that cultural exchange is minimal, conceivably become the nucleus for a new tribe. We have documented the fact that these fissions—as might be expected but must be demonstrated—are along kinship lines, leading to a highly nonrandom sampling of the gene pool. Thus, Sebastião's band of 90 persons, who finally "settled down" at São Marcos (Salzano *et al.*, 1967) probably represented less than half that many independent genotypes. The term *fission-fusion* has been applied to these events (Neel and Salzano, 1964).

On a long-term basis, this population structure may have many of the mathematical consequences of any one of several other population models which have been suggested. Instead of individuals, the unit of diffusion is a group of related individuals; instead of a regular distance function describing the migration, there is an irregular function which requires that on a time span of 5–10 generations, the whole tribe be viewed as the breeding unit. But human evolution may also be viewed as a series of short-range events, many of them individually improbable and structured by aspects of the system, and then the departures from a hypothetical large scale equilibrium at any point in time may become important. It is in this connection worth bearing in mind how small the hominoid population of the earth may have been 500,000 to 1,000,000 years ago (cf. Deevy, 1960).

One example of the consequences of this structure is that, with respect to the process whereby new population units ("tribes") evolve from old, the original sampling event would appear to increase the probability that, at the outset, new combinations of gene frequencies will be explored, but, with the entire tribe the ultimate breeding unit, the effective population size will usually become such that over a sufficient interval of time deterministic rather than nondeterministic genetic events will control subsequent developments within the tribe. This structure appears in general to correspond to that repeatedly visualized by Wright (1931 *et seq.*; cf. especially 1966) as most compatible with rapid and effective evolution, with the reservation that the amount of exchange at the tribal interface (migration), a factor of great importance in Wright's formulation, remains uninvestigated. Whether, as Wynne-Edwards (1962) maintains, at this cultural level the social structure within the population subunits ("villages") is such as to encourage "group selection" is quite another question, on which the available evidence does not yet permit an opinion.

A second example of a possible consequence of this population structure issues from the work of Fraser *et al.* (1967), who by simulation procedures have shown that the establishment of inversion polymorphisms is markedly frequency-dependent under schemes of normalizing selection. For instance, one particular inversion (on a six-locus model) needs to exceed a critical frequency of approximately 0.10 for the establishment of a stable polymorphism. It is evident that the same scheme of selection acting on a multiple allelic series will lead to the same type of frequency dependence. The combination of differential fertility and the tendency of related persons to join together in a village fission provides a mechanism for marked increases in gene frequencies in small populations on the basis of chance alone; i.e., a chance increase from 0.01 to 0.10 (the critical level) is by no means inconceivable. Once the polymorphism increases to an equilibrium value of, say, a gene frequency of 0.50, the pattern of fission-fusion would seem to provide the basis for what might be termed a genetic chain reaction, as in successive villages the critical frequency is exceeded by the addition of groups of people from villages in which the polymorphism is already established.

There are two major unknowns in our knowledge of the Xavante population structure. One is the extent in former times of the genetic exchange at the interface between tribes. The capture of women and children was (and still is) a primary objective in the warfare of many Indian tribes. But the numerical aspects of this phenomenon will be extremely difficult to quantitate. The second unknown is the extent to which the present internal mobility of the

Xavante is in response to the external pressures of advancing civilization. Studies of other suitable tribes are necessary to an opinion on this score.

B. THE EVENTS WHICH LEAD TO THE FORMATION OF A NEW TRIBE MAY BE SUCH THAT GENE FREQUENCY DIFFERENCES BETWEEN "RELATED" OR EVEN LONG SEPARATED TRIBES WILL USUALLY NOT BE PRIMARILY THE RESULT OF SELECTION.

This is implicit in our first proposition but needs explicit statement. The kind of sampling process of the "tribal genome" which the study of the Xavantes suggests may be the basis for the nucleus of a new tribe has a high probability of resulting in a situation rather distant from equilibrium for some loci. Subsequent selection plus exchanges with other breeding units should result in a convergence towards equilibrium gene frequencies. But it seems very likely that at any point in the time-space continuum, the local residential groups (commonly termed villages) of which a tribe is composed will often not be in genetic equilibrium, and mean gene frequency differences between tribes related by descent are as apt to be due to chance as to an expression of selective differentials (cf. Ride, 1934). The inference is that much selection is concerned with undoing chance departures from genetic equilibrium; to the genetic "loads" imposed by mutation, segregation, recombination, substitution, incompatibility, and migration, we must add a "sampling" load (cf. Kimura and Crow, 1964; Crow and Kimura, 1965) which, if one regards the village as the breeding unit, may outweigh all the others in its significance.

The foregoing heavily emphasizes what we shall term the *lineal effect* but of course does not preclude the role of subsequent genetic drift in the early generations of "tribalization," while population numbers are still building up. On the other hand, questions are raised concerning the evaluation of the role of drift. For instance, Cavalli-Sforza *et al.* (1964, 1965) in an elegant analysis have demonstrated that the genetic differences between villages in the Upper Parma Valley can be adequately explained by the operation of drift alone. Their approach appears to assume that the initial gene frequencies in the villages of the valley were similar if not identical. While we hesitate to compare the colonization of an Italian valley with the internal readjustments of the Xavante, it may be that there are certain principles in the extension of human populations which are remarkably similar the world over.

We note in passing that the term *founder effect* as currently employed with reference to human populations does not seem to distinguish between two quite different phenomena, namely, the "luck" of a small but random draw from a population and the nonrandom draw that occurs because, in the process by which new social (hence biological) groups are formed, aspects of the social organization of the group in question (e.g., lineal descent) may be an important factor in determining the composition of the new group (see also Hunt, 1950; Giles *et al.*, 1966). This phenomenon has not yet been adequately incorporated into the conceptual framework of population genetics. The observations of Turnbull (1965) on the Pygmies of the Ituri Forest region make it clear that these fission-fusion events are not confined to the American Indian.

C. MANY OF THE APPARENT GENETIC DIFFERENCES BETWEEN INDIAN TRIBES WHICH EMERGE FROM A SURVEY OF THE LITERATURE ARE PROBABLY SPURIOUS, A RESULT OF INADEQUATE SAMPLING AND TECHNICAL ERROR; CONVERSELY, APPARENT SIMILARITIES MUST BE SUBJECT TO THE SAME RESERVATIONS.

This point will be considered *in extenso* in subsequent papers dealing with the taxonomy of the American Indian, but must be mentioned here as an important outgrowth of these studies. The frequency of the *NS* gene was 0.15 at São Marcos but 0.01 at Simões Lopes, while the R^2 gene constituted 0.39 of the pool at São Domingos but 0.24 at Simões Lopes (Gershowitz *et al.*, 1967). More strikingly, the Inv^1 gene had a frequency of 0.37 at São Marcos but 0.63 at Simões Lopes (Shreffler and Steinberg, 1967). Thus, choice of village would influence the estimate of Xavante gene frequencies.

Kraus and White (1956) directed attention to similar but less marked "microevolution" among the Western Apache of Arizona and stressed the sampling problems in estimating tribal gene frequencies. Similar but usually less marked examples of "internal differentiation" have been reported, *inter alia*, among the Navajo Indians of the Southwestern United States (Brown *et al.*, 1958), the Caingang Indians of Southern Brazil (Salzano, 1961b), the Pemon Indians of Southeastern Venezuela (Layrisse *et al.*, 1962), the Tzotzil of Southern Mexico (Matson and Swanson, 1963) and the Eastern Algonkians (the Naskapi and Montagnais) of Canada (Blumberg *et al.*, 1964). With the exception of the Pemons, all these groups are sufficiently acculturated or settled (on reservations) that one wonders to what extent the original picture has been altered. Recently, an even more striking example has been recorded among the relatively undisturbed Yanomama of the Upper Orinoco Region of Venezuela (Arends *et al.*, 1967). Evidence suggesting similar "village" differences has been encountered in other tribal-type ethnic groups, as, for example, within the subdivisions of the Malayan aborigines (Polunin and Sneath, 1953) and Melanesian linguistic groups (Simmons *et al.*, 1964, 1965; Curtain *et al.*, 1965; Giles *et al.*, 1966; see also Simmons *et al.*, 1962). The Eskimo populations would seem to provide an additional albeit somewhat "special" example of this phenomenon (Laughlin, 1950).

These real variations, in the sense that they are encountered by the same observers using identical techniques, are magnified by technical factors. The magnitude of these technical errors even under favorable circumstances has been pointed out by Neel *et al.* (1964; see also Osborne, 1958; Ellis *et al.*, 1963). How much greater the error may be under unfavorable circumstances—prolonged transport and storage of blood, poor antisera, and inexperience—can only be the subject of conjecture. We are also concerned that Caucasian-derived antisera which yield clear-cut results with Caucasian erythrocytes may not be equally efficient with Indian bloods. Thus, apparent differences in gene frequencies between tribes of 0.1 or even 0.2 may be spurious if sampling and technical procedures are inadequate.

Furthermore, if one is interested in the genetic affinities of the various

Indian tribes, an apparently insoluble problem for some tribes is the "representativeness," with respect to a given tribe, of those groups who survived the decimations of 1500 to 1900. If entire villages were wiped out, how well even in the absence of changes in gene frequency due to recent selection do the survivors of those villages which were not exterminated reflect the precontact total gene pool of the tribe? Apparent genetic differences between Indian tribes must be regarded as spurious until rigorously confirmed. Clearly, the differences in A-O type frequencies between the tribes of North and South America (reviewed in Mourant and Kopec, 1958) and in Diego type frequencies between South American tribes (reviewed in Layrisse and Wilbert, 1960) are real, but, beyond this, caution is indicated. There is thus not only the need for additional studies on a number of tribes already investigated but also a careful consideration, before efforts are made to relate a tribe to other tribes, of its detailed history. Finally, in the face of these variables, it will be a brave man who, in considering the genetic taxonomy of a specific group such as the American Indian or the Polynesians, will accept the added variable of a substantial racial admixture.

D. THE AMOUNT OF GENETIC VARIABILITY IN THE VILLAGES OF THIS "SMALL, ISOLATED, INBRED" TRIBE IS SIMILAR TO THAT IN A CONTEMPORARY URBAN POPULATION.

There are numerous remarks in both the popular and anthropological literature about the striking similarities in appearance and lack of variation in some of the remote Indian tribes. We have systematically sought to explore the extent of the genetic variation in the Xavantes. All of the recognized major genetic polymorphisms are represented except for those absent in South American Indians in general, namely, polymorphisms of the ABO and Kell groups, the hemoglobins, and G6PD deficiency (Gershowitz *et al.*, 1967; Shreffler and Steinberg, 1967; Tashian *et al.*, 1967). The studies of the urine reveal suggestive evidence of several possible carrier states (Neel *et al.*, 1967). By a semiobjective and quantitative approach, the morphological, dental, and dermatoglyphic variation in the Xavante is somewhat less than in a sample of unrelated persons from the cosmopolitan population of Hamburg, Germany (Niswander *et al.*, 1967). For these latter traits, lack of knowledge of the correspondence between genotype and phenotype, plus the probable greater uniformity of the environmental factor for the Xavante, as well as the inclusion of some related individuals in the Xavante series (otherwise no series could be assembled) prevent meaningful, precise contrasts of the "amount" of variation; on an intuitive basis, we are impressed that it is so great. Although it is true that among the Xavante (and other Indian tribes) there is relative homogeneity with respect to skin, hair, and eye color (Neel *et al.*, 1964), even for skin color careful measurements reveal appreciable variation in some tribes; unfortunately (for the sake of the argument) the environmental contribution to this variation may be considerable (Keiter and Salzano, 1963; Harrison and Salzano, 1966).

It is now clear that genetic polymorphisms are to be found at a substantial proportion of all loci in organisms as diverse as Drosophila (Hubby and Lewontin, 1966; Lewontin and Hubby, 1966) and man (Harris, 1966). Without question, the focal problem in human population genetics today is to understand the biological significance of the many polymorphisms now recognized —as well as those almost certainly awaiting discovery. If, on the one hand, they are maintained by selection, then, as genetic loads have been formulated, the *burden* the polymorphisms would appear to impose on a population is of such a magnitude as to require reconsideration of load theory. If, on the other hand, the polymorphisms are neutral, it is difficult to understand the occurrence of *specific* polymorphisms in such a variety of populations (as opposed to the accumulation at each locus of many mutant genes because of simple mutation pressure). Between these two polarizations there are of course many intermediate possibilities. The present observations on the Xavante underscore this growing dilemma. The breeding structure of this group would appear to favor the loss of genes without selective significance. On the other hand, when nongenetic deaths, deaths from dominant mutations, and deaths from chromosomal abnormalities are subtracted from postfertilization, prereproductive mortality in the Xavante and other similar groups, is there sufficient mortality left to balance and stabilize these numbers of polymorphisms, if they are visualized as functioning in independence of one another? The recent papers of Sved *et al.* (1967), King (1967), and Milkman (1967) would appear to initiate a much needed reappraisal of load theory. As this reappraisal proceeds, the need for accurate data on the population structure of primitive groups is obvious if we are to understand the maintenance of the polymorphisms.

E. DESPITE THE ABSENCE OF STERILITY IN THE XAVANTE, THE MEAN NUMBER OF BIRTHS TO WOMEN WHO HAVE COMPLETED REPRODUCTION IS LESS THAN IN MANY AGRICULTURAL SOCIETIES; TO WHAT EXTENT THIS PHENOMENON IS PHYSIOLOGICAL AND TO WHAT EXTENT VOLUNTARY IS NOT CLEAR.

In the Hutterites, with early marriage, relative absence of venereal disease, and an outlook that places a premium on large numbers of children, the mean number of livebirths per woman reaching the age of 45 and its standard deviation is 9.0 ± 3.7 (Eaton and Mayer, 1953). The estimate of the corresponding figure for Xavante women is 5.7 ± 2.4. This is less than that of the recently acculturated Caingang (6.6 ± 3.8; Salzano, 1961a, 1964) or of women in such established agricultural economies as East Pakistan (6.5 ± 3.2; Aird, 1957) or Ghana (7.0 ± 3.3; Fortes, 1954), despite somewhat more infertility in these latter two groups.

There are no data on the ovulatory cycle of the Xavante, nor the extent to which the custom of nursing children for several years suppresses ovulation. Neither are there precise data on the age at menopause. But while it is possible that biological factors tend to limit fertility, there is also evidence for sociological factors. Among many Indian tribes of this region, there is abundant anecdotal evidence for abstinence from intercourse for a prolonged period following birth of a child, use of herbs to prevent conception, and induction of abortion by herbs or trauma. Furthermore, infanticide may be practiced.

Unfortunately, we can find no quantitative data on the frequency and/or efficacy of these methods. To what extent these self-imposed restraints on reproduction are due to real or fancied limitations in the food supply or, as seems at least as important on the basis of our contacts, the need for remaining mobile is unclear. But at a time when the world is increasingly concerned with fitting its numbers to its resources, it is cause for contemplation that these "primitive" people have met the issue of reconciling numbers to resources and way of life. Our knowledge of how this is accomplished is very imperfect; it will be an objective of future studies to acquire better understanding of this matter.

Although there is a dearth of precise statistics, the very limited data available suggest that such intermediate fertilities characterize many primitive people (cf. Krzywicki, 1934). Only with the development of agriculture and the advent of religions stressing how pleasing fruitfulness was to the gods did the pattern change. It is tempting to speculate that simply providing the means of population regulation will not solve the current problems—only when all the religions and all the governments concerned create the necessary intellectual acceptance and commitment will population control be achieved.

F. THE VARIANCE OF MALE FERTILITY AND OF SURVIVING CHILDREN PER POSTREPRODUCTIVE MALE IS APPROXIMATELY TWICE AS GREAT AS FOR FEMALES, WITH, IN VIEW OF THE SOCIAL STRUCTURE OF THE XAVANTE, THE INFERENCE THAT MALE FERTILITY DIFFERENTIALS MAY OFFER A GREATER OPPORTUNITY FOR SELECTION THAN FEMALE.

The variance for number of surviving children to Xavante women 40 years of age and over is 3.9. This variance is relatively less than for any other population for which we have data, in part due to the virtual absence of sterility in this group. The corresponding figure for males is 12.1. However, this tentative figure is strongly influenced by one unusually prolific male; when he is eliminated from the calculation, the male figure is 5.9. This difference between the sexes is, of course, due to the institution of polygyny.

From the genetic standpoint, a high frequency of nonpaternity would complicate the interpretation of the apparently greater variance of males than females with respect to fertility and surviving offspring. In an earlier paper (Shreffler and Steinberg, 1967), it has been reported that among 107 mother-father-child combinations, there were nine apparent exclusions. If one were dealing with a large population, one would proceed from this observation to a calculation of the theoretical frequency of nonparentage. As pointed out earlier, the intricacies of the kinship system and the language barriers are such that confusion concerning maternity is possible, and in fact we recognize one such case.

Even if maternity were certain, the statistical conventions on which calculations of nonpaternity are based do not apply here. Thus, an underlying assumption in the calculations usually employed is absence of inbreeding, whereas, as demonstrated earlier, inbreeding is relatively common in this group. MacCluer and Schull (1963) have presented an extension of the usual methods for calculating nonpaternity, which takes the possibility of inbreeding into consideration for individual father-mother-child trios (but not for sibships nor three-generation data). However, no statistical method has been developed to take into consideration the possibility of preferential nonpaternity, such as would result from wife-lending to brothers, which occurs in many Indian groups.

But while a precise calculation seems impossible, the data can fix an order of magnitude—and this was our objective. The literature of the cultural anthropologist on the sexual behavior of the Indian is replete with reference to seduction, wife-lending, and ceremonial rape, to the point where one could easily assume mating is almost at random. The resulting conceptions could either increase or decrease the variance of male reproductive indices, depending on which males were responsible. We feel these data indicate that among the Xavante the bonds of matrimony are sufficiently well observed that the differences between male and female variances described above are valid.

Among the Xavante, the number of wives is a measure of social status (Maybury-Lewis, 1967). This was true for other Indian groups (e.g., Hallowell, 1938; Levi-Strauss, 1944; Dunning, 1959) and may have been a feature of the breeding structure of many or most primitive groups (e.g., Eskimos: Jenness, 1922; Dunning, 1962). This social status is usually earned; hunting-gathering-incipient agriculture Indian societies were relatively democratic and equal in opportunity (cf. Hallowell, 1963). In general, the leaders will be accomplished orators, good hunters and warriors, well versed in the tribal lore. In these small communities, one's performance under widely varying conditions is well known; it seems reasonable to postulate that the leaders will tend to have intellects and physiques which in that culture are superior.

A simple model will forcibly illustrate the potential genetic significance of this social structure, especially as contrasted to the practices of most advanced societies. Let us assume an Indian population of only 100 persons, evenly distributed in two generations (parents-children), in which the mean I.Q. of the parent generation is 100, and with numbers remaining constant generation after generation. Assume that by virtue of polygyny two leaders of I.Q. 110 leave eight children, the rest of the next generation being contributed by the remainder (with I.Q. 99.6). We submit that the man who acquires multiple wives at this cultural level has manipulated the system no less than the man who through his own initiative has built a business or acquired large estates in our culture. If the I.Q. of the chief's children is at the midpoint of the parents (simple additive inheritance) then the mean I.Q. of the following generation is 100.4. If for the next generation the two chiefs again average 10 I.Q. points higher than the remainder and reproduce as before, mean I.Q. now increases to 100.8.

We do not mean literally to suggest so simple or rapid an increase. Thus, to mention only one disturbing factor in this simple scheme, these hypothetical gains from selection must be balanced against loss from mutation; there are no data on the importance of this phenomenon. On the other hand, the possibilities for selection inherent in this system of mating are clear. A primary objective of future studies will be a systematic contrast of the attributes of polygynous and nonpolygynous males in as many respects as possible. The attributes of their wives will also be studied, for possible evidences of "discriminative passivity" (cf. Dobzhansky, 1962).

G. IF THE XAVANTE BREEDING STRUCTURE IS TYPICAL OF EARLY HUMAN POPULATIONS, IT SEEMS UNLIKELY THAT DIFFERING EXPOSURES TO THE INBREEDING BOTTLENECK ACCOUNT FOR THE APPARENT DIFFERENCES IN CONSANGUINITY EFFECTS BETWEEN DIVERSE POPULATIONS.

For reasons detailed in Salzano *et al.* (1967), it has proven extremely difficult to estimate inbreeding levels in this group. Although Allen's suggestion (1965) that comparisons of inbreeding between populations should be based on a uniform referent generation has much to recommend it, at this level of culture even the "minimal" comparison, based on grandparental generation, could be applied to only 7.0% of all marriages. There is no way to judge how biased a sample this 7.0% might be. New approaches to the estimation of inbreeding coefficients are badly needed.

Recently Yasuda (1966) has presented an ingenious method for the estimation of inbreeding levels in populations, based (among other things) on the excess over expectation from random mating of genotypic similarity among parents. We are indebted to Professor C. A. B. Smith for pointing out that, whatever the merits of this method when applied to large populations, it appears to have severe limitations when utilized for small populations, where random mating may result in an appreciable probability of marrying a near relative. Thus, in a small population in which a high proportion of individuals have one or more common ancestors but in which mating is approximately at random, the degree of consanguinity will not be reflected in the departure from Hardy-Weinberg equilibrium. Furthermore, as Wahlund (1928) has pointed out and Yasuda himself emphasizes, heterogeneity and stratification may lead to departures from Hardy-Weinberg not due to consanguinity in both large and small populations.

Our present "best" approximation to the mean coefficient of inbreeding in this group is 0.02 to 0.03, i.e., the average marriage corresponds to second cousins or first cousins once removed. If this is a high estimate, the argument that follows is only strengthened. What are the implications of such levels of inbreeding for the elimination of highly deleterious recessive genes? In Drosophila, the "average" highly deleterious "recessive" gene (newly arisen; radiation-induced) appears to carry a selective disadvantage in the heterozygote of approximately 0.05 (discussion in Muller, 1950), the precise amount undoubtedly varying with environmental conditions. Spontaneously arisen recessive deleterious mutations extracted from wild populations also tend to show such heterozygote effects, although there is disagreement concerning the exact proportion that do so (references in Crow and Temin, 1964; Wallace, 1965). Preliminary data on the mouse fail to show dominant deleterious effects for radiation-induced recessive lethals (Lüning and Sheridan, 1966), but, with the growing evidence for heterozygote effects in man, for the moment we assume a comparable figure for newly arisen spontaneous mutations in man. If this assumption is incorrect, then, of course, the argument that follows is invalid.

At equilibrium in a population with inbreeding (Crow and Temin, 1964),

$$m[1-(1-f_1)\ (1-F)q]=q^2+q[F\ (1-q)+(1-f_1)\ (1-F)\ (1-2q)]$$

where

q = the frequency of the gene in question,
m = mutation rate, here assumed to be 0.00001/gene/generation,
f_1 = the fertility of the heterozygote, assumed to be 0.95,
F = mean coefficient of inbreeding, assumed to be 0.03,

and the fertility of the homozygote is assumed to be 0.0 (an assumption that maximizes the role of inbreeding).

How effective are the Xavante levels of inbreeding in eliminating "recessive" genes? In the foregoing example, the equilibrium value of q is 0.00013. Even in this extreme example, the ratio of elimination in heterozygotes to elimination in homozygotes, $[0.0485q(1-q)]/[0.0300q(1-q)+q^2]$, is greater than 1.0. By contrast, in a population in genetic equilibrium with low levels of inbreeding ($F = 0.001$), the equilibrium value of q would be 0.00020. In first cousin marriages from the former population, the frequency of recessives would be 0.0000078, whereas from the latter, 0.0000124. Inbreeding effects would be greater in the latter population, but even under these extreme assumptions, only some 50% more. Substitution of other reasonable values in the equation leads to the same general conclusion.

Accordingly, it seems unlikely that apparent differences between populations in the magnitude of observed inbreeding effects (reviewed in Schull and Neel, 1965) are to any significant degree to be related to differences in the inbreeding histories of the populations, i.e., the inbreeding bottleneck which can be invoked to explain apparent differences in inbreeding effects between populations (cf. discussion in Schull, 1963) seems in fact unlikely to have played a significant role.

A difficulty in the foregoing calculation—and the same kind of difficulty which has arisen repeatedly in these presentations—is the propriety of applying large sample statistics to small populations, even for the sake of an illustration. Thus, at $q = 0.0002$, a given gene will be completely lacking in the vast majority of subpopulations but, in the subpopulation (village) where it is present, may have a frequency such that homozygous elimination is more common than the above calculations would suggest. Otherwise stated, it would appear that a gene arising in some one of a number of small endogamous populations [with "random" inbreeding in the sense of Allen (1965)] will have a higher probability of being eliminated in the homozygous condition than the same gene in a larger, panmictic population whose numbers equal those of all the small populations combined. That even in large and apparently relatively homogeneous populations there may persist marked local variations in the frequency of a recessive gene has been well demonstrated for the acatalasemia gene in Japan; the consequences of this uneven distribution for inferences based on the inbreeding effect may be considerable

(Hamilton *et al.*, 1961). Although this *deme effect* is in the final analysis the result of inbreeding, this is not the inbreeding bottleneck as the term has been used.

H. THERE IS AN UNRESOLVED PARADOX BETWEEN THE APPARENTLY EXCELLENT HEALTH OF THE YOUNG XAVANTE AND THE RELATIVE ABSENCE OF ELDERLY INDIVIDUALS.

The extent and type of competition among individuals at these cultural levels, a subject of profound genetic interest, is intimately related to health. The young Xavante is a superb physical specimen. Health is more than freedom from disease. An American population is healthy but fails to project the sense of feral vitality and physical resilience of the Xavante. There are differences by the more objective criteria we attempt to use—specifically, the musculature, the keen vision, the lack of dental caries, the slow pulses, and low blood pressures—but these tell only a fraction of the story. Under these circumstances, the relative absence of individuals over 40 years of age is one of the most troublesome observations to emerge from this study. In the case of the males, a possible partial explanation lies in the high risk of traumatic death, but this explanation does not seem equally applicable to females.

One must be careful in extrapolating from this or any other Indian population to primitive men in general. Thus, it is possible that in his northern entry into the Americas, the ancestor of the Indian succeeded in leaving behind many of the diseases with which he had been afflicted. The other primitive groups to which we might turn for a possibly "older" picture unfortunately usually have been sufficiently disturbed that one doubts their suitability and, with rare exceptions, such as the excellent study of Polunin and Sneath (1953), have not often been evaluated in such a way that we can reach over-all judgments concerning health. Under these circumstances, skeletal remains can be helpful, although the possibility that the remains of children, especially the very young, are not preserved as carefully as those of adults must always be borne in mind. Be this as it may, the estimated ages of Paleolithic and Mesolithic skeletons are remarkably similar to the estimated ages of the Xavantes (Vallois, 1937, 1960; other references in Genovés, 1963). There is the same paucity of individuals over 40, while the relatively low proportion of young skeletons suggests that, as in the Xavante, mortality during childhood was intermediate (cf. Brothwell, 1963). The degenerative diseases of old age have played little role in the medical burdens of primitive man (cf. also Dunn, 1967). In theory, the study of palaeopathology should help establish the extent to which some of the disease patterns of current primitive groups are the same as those of prehistorical primitive groups and so provide insight into the propriety of extrapolating from present-day to previous primitive populations; in fact, as a recent symposium illustrates (Jarcho, 1966), this field of inquiry is confronted by many problems.

Much has been written concerning the rapid deterioration in health which ensues as primitive man becomes acculturated; the observations of Polunin and Sneath (1953) on the Malaysian aborigines constitutes one of the best documentations to date. To an extent, this finds a satisfactory explanation in impaired nutrition, the introduction of "new" diseases to a totally nonimmune population, alcoholism, and a change in attitude, which, however poorly understood, certainly influences the probability of an unfavorable outcome in cases of illness. However, there are additional aspects of this transition, of particular interest to the geneticist. Consider the well documented decrease in visual acuity with civilization (Post, 1962), the less well-established greater frequency of deviated nasal septum with nasal obstruction (Post, 1966), and the possible but still unstudied increase in malocclusion of the bite. The extent to which these changes are genetic is unclear. The observations on the Bakairi (Niswander, 1967) suggest the changes may be more rapid than can reasonably be ascribed to the effects of relaxed selection. We suggest that in the specific case of visual acuity, deviated septum, and malocclusion these changes may not be unrelated, but rather interdependent manifestations of some measurable change(s) in the facial complex in which both genetic and dietary factors play a role. This aspect of the effect of cultural change is subject to study and could serve as a prototype for a number of related problems. Thus, careful observations of the rapidity with which these effects emerge with acculturation not only will help distinguish between genetic and nongenetic etiologies but also will provide guidance concerning reversibility. A similar problem may exist at a biochemical level with respect to the hyperuricemia observed in the Xavante (Neel *et al.*, 1967). The other, more acculturated groups of American Indians studied in this respect do not exhibit hyperuricemia (Ford and de Mos, 1964; O'Brien *et al.*, 1966). To what extent are the high uric acid values genetic and to what extent environmental? How will they change with acculturation?

I. THE INTERACTION BETWEEN MAN AND AGENTS OF DISEASE AT THIS CULTURAL LEVEL MAY DIFFER IN IMPORTANT RESPECTS FROM THE MORE FAMILIAR INTERACTIONS OF CIVILIZED POPULATIONS.

Antibodies to a wide variety of agents of disease have been demonstrated in this population (Andrade *et al.*, 1967). Some of these agents are very likely introduced (measles, pertussis) but others (Salmonella, poliomyelitis, and certain arboviruses) are endemic. The inventory is of course only beginning. Likewise, the presence of a wide variety of endemic intestinal parasites has been demonstrated (Neel *et al.*, 1967). Yet, as we have been at pains to point out, these do not seem to be disease ridden populations in the usual sense of the word. One has the feeling that in civilized populations the acquisition of antibodies to these endemic agents and the presence of these parasites would have exacted a heavier toll in morbidity and mortality than seems to be the case here.

We would like at this time to reiterate an earlier suggestion, that the acquisition of these antibodies may have been accompanied by less "clinical" illness than the experience of civilized populations would suggest (Neel *et al.*, 1964). Otherwise stated, primitive man was in a better equilibrium with his environment than is civilized man. The intimate contact of the child with his environment ensures an early introduction to many pathogens—the high level of maternal gamma globulin available for placental transfer and the prolonged period of nursing may obtund the first contacts with these pathogens and permit a relatively smooth transition from passive to active immunity against many pathogens. The recent demonstration by Kenny *et al.* (1967) of bacterial and viral coproantibodies in breast-fed infants supplies important new evidence concerning the validity of this suggestion.

However, the question of a different balance between man and his pathogens at this level undoubtedly has many additional facets. Thus, Dubos (1965) has recently summarized the information relating intestinal flora, diet, and health. The balance between "pathogens" and "normal inhabitants" of the large and small intestine is both complex and still very poorly understood. The shifts in composition of bacterial flora with changes in diet may result in imbalances with unfavorable consequences for health. The beneficial effect on the child of prolonged breast feeding may be as closely related to the resulting high lactobacillus count in the intestinal flora as to the precise balance of nutrients in human milk.

An extreme example of this possibility may be tropical sprue—the observation by Guerra *et al.* (1965) of the response of this entity to long-term antibiotic therapy, together with the other characteristics of the disease, raises the question of a bacterial imbalance related to the type of diet commonly consumed in the tropics by socioeconomically disadvantaged groups. Along these same lines, it is possible that some of the pathogenic intestinal parasites and bacteria for whose occurrence we have evidence in the Xavante are to a considerable extent held in check by other components of the intestinal flora. The pertinence of these possibilities to genetic problems has recently been well emphasized by Otten (1967) in her discussion of the distribution of microbial and human blood group antigens and antibodies. An experiment for the future is a comparison of the results of inoculation of germ-free mice or other suitable mammals with fecal suspensions from such a group as the Xavantes and from a highly civilized group.

One of the basic questions in human epidemiology is the specificity of genetically-determined disease resistance. Recently, stimulated in part by the relationship between the sickle cell trait and susceptibility to falciparum malaria, a number of attempts have been made to relate other specific genes of man to resistance to certain diseases or their sequelae (references in Vogel *et al.*, 1960; Motulsky, 1960; Livingstone, 1960; Azevêdo *et al.*, 1964; Gershowitz and Neel, 1965; Chung *et al.*, 1965; Otten, 1967). The experimental evidence from laboratory mammals reveals a high degree of specificity in genetically determined resistance to many infectious agents but yet significant cross-resistance to pathogens related to those for which selection has been exercised (Webster, 1932; Sabin, 1954; further references in Motulsky, 1960; Schull, 1963). The observations on primitive man suggest that a high level of challenge of immunological competence by a variety of pathogens has been a feature of human existence for a long time. If so, then the great epidemics of historical times, whose importance as agents of selection has been stressed by

Haldane (1949, 1957) and Motulsky (1960), would introduce a new factor into selection in proportion to the relationship of the pathogen concerned to other pathogens to which the species has previously been exposed. For instance, one might expect the American Indian to have relative resistance to "new" arbor or enteric viruses but perhaps not to respiratory viruses. Since most of the polymorphisms are well established in primitive men, including populations not known to have been visited until recently by the epidemic diseases of civilization, it would seem that, despite the many inherent difficulties, an effort must be made to find evidence at this level for the action of selection if the total significance of the polymorphisms is to be understood. It may be noted that the findings regarding antibodies only intensifies the mystery of the relative absence of aged in this population. One would presume that by adulthood repeated exposure would have resulted in a lasting immunity to the majority of the important agents of disease in the environment.

Dunn (1967) has recently emphasized the diversity of the ecosystems occupied by primitive man, with the corollary that the "patterning" of disease will vary greatly from one group to another, as illustrated by the difference in the intestinal parasitism of African Bushmen and Malayan aborigines. While agreeing with this point, we wonder whether the intimate relationship of the hunter-gatherer-incipient agriculturalist with his environment, so rightly emphasized by Dunn, may not introduce an epidemiological consideration which will influence the host-pathogen relationship in widely diverse environments.

We close this section by agreeing with Dubos (1965) that:

> It is almost certain, in fact, that medicine will eventually flounder in a sea of irrelevancy unless it learns more of the relations of the body machine to the total environment, as well as to the past and the aspirations of human beings. The study of such problems will require the development of scientific methods far more sophisticated than those which constitute today the stock in trade of orthodox natural sciences. What is needed is nothing less than a new methodology to acquire objective knowledge concerning the highest manifestation of life—the humanness of man.

In the field of biochemical genetics the current shift in emphasis, from understanding structural genes to understanding the mechanisms of genetic control, requires no comment. Human population genetics is undergoing a similar transition, from counting genes in populations to an effort to understand regulatory mechanisms in actual populations. The difficulty in obtaining meaningful insights is matched only by the importance of the problem. The future of efforts to utilize genetic knowledge for the good of man lies far less in the spectaculars of applying transduction, transformation, or cloning techniques to man than in the acquisition of the kind of understanding of genetic population dynamics which will permit man to develop the society most consistent with both his present genetic endowment and his continuing evolution. This will be possible only from patient, laborious, and extensive studies of human populations, with groups such as are under discussion here almost certainly providing some of the key insights, if only because the study of relatively simple systems should help us understand the more complex. It is a sobering fact that if, as seems likely, the genetic polymorphisms are a significant feature—perhaps *the* significant feature—of the genetic integrity of human populations, for not a single one of the rapidly mounting list of polymorphisms (including the sickle cell polymorphism) do we fully understand the dynamics of the situation. The history of attempts at control without understanding leaves no room for doubt as to the wisdom of bending all possible efforts to comprehend the genetic structure of human populations before moving to change that structure.

REFERENCES

Aird, J. S. 1957. *Fertility Levels and Differentials in Two Bengali Villages.* Doctoral Thesis, University of Michigan.

Allen, G. 1965. Random and nonrandom inbreeding. *Eugenics Quart.* 12: 181–198.

Andrade, A. H. P., Brown, G. E., Eveland, W. C., Goober, J., Neel, J. V., Sodeman, W. A., Stollerman, G. H., Weinstein, E. D., and Wheeler, A. H. 1967. Further studies on the Xavante Indians. X. Occurrence of selected antibodies. (Manuscript.)

Arends, T., Brewer, G., Chagnon, N., Gallango, M., Gershowitz, H., Layrisse, M., Neel, J., Shreffler, D., Tashian, R., and Weitkamp, L. 1967. Intratribal genetic differentiation among the Yanomama Indians of Southern Venezuela. *Proc. Natl. Acad. Sci.* (U. S.) 57: 1252–1259.

Azevedo, E., Krieger, H., and Morton, N. E. 1964. Smallpox and the ABO blood groups in Brazil. *Amer. J. Hum. Genet.* 16: 451–454.

Blumberg, B. S., Martin, J. R., Allen, F. H., Jr., Weiner, J. L., Vitagliano, E., and Cooke, A. 1964. Blood groups of the Naskapi and Montagnais Indians of Schefferville, Quebec. *Hum. Biol.* 36: 263–272.

Brothwell, D. 1963. The biology of earlier human populations. In *Science in Archeology,* D. Brothwell and E. Higgs (eds.). New York: Basic Books, Inc., pp. 325–329.

Brown, K. S., Hanna, B. L., Dahlberg, A. A., and Strandskov, H. H. 1958. The distribution of blood group alleles among Indians of Southwest North America. *Amer. J. Hum. Genet.* 10: 175–195.

Cavalli-Sforza, L. L., Barrai, I., and Edwards, A. W. F. 1964. Analysis of human evolution under random genetic drift. *Cold Spring Harbor Symp. Quant. Biol.* 29: 9–20.

Cavalli-Sforza, L. L., and Edwards, A. W. F. 1965. Analysis of human evolution. In *Genetics Today* (Proceedings of the XI International Congress of Genetics, The Hague, The Netherlands, September, 1963), Vol. 3, S. J. Geerts (ed.). Oxford: Pergamon Press, pp. 923–933.

Chung, C. S., Pitt, E. L., and Dublin, T. D. 1965. Heterozygous ABH secretor and susceptibility to rheumatic fever. *Amer. J. Hum. Genet.* 17: 352–358.

Crow, J. F., and Kimura, M. 1965. The theory of genetic loads. In *Genetics Today* (Proceedings of the XI International Congress of Genetics, The Hague, The Netherlands, September, 1963), Vol. 3, S. J. Geerts (ed.). Oxford: Pergamon Press, pp. 495–506.

Crow, J. F., and Temin, R. G. 1964. Evidence for the partial dominance of recessive lethal genes in natural populations of Drosophila. *Amer. Naturalist* 98: 21–33.

Curtain, C. C., Gajdusek, D. C., Kidson, C., Gorman, J. G., Champness, L. T., and Rodrigue, R. 1965. Haptoglobins and transferrins in Melanesia: Relation to hemoglobin, serum haptoglobin and serum iron levels in population groups in Papua—New Guinea. *Amer. J. Phys. Anthropol.* 23: 363–380.

Deevey, E. S. 1960. The human population. *Sci. Amer.* 203: 195–204.

Dobzhansky, T. 1962. *Mankind Evolving.* New Haven: Yale University Press.

Dubos, R. 1965. *Man Adapting.* New Haven: Yale University Press.

Dunn, F. L. 1967. Epidemiological factors: Health and disease in hunter-gatherers. In: *Man the Hunter.* (In press).

Dunning, R. W. 1959. *Social and Economic Change Among the Northern Ojibwa.* Toronto: University of Toronto Press.

Dunning, R. W. 1962. An aspect of recent Eskimo polygyny and wife-lending in the eastern Arctic. *Human Organization* 21: 17–24.

Eaton, J. W., and Mayer, A. J. 1953. The social biology of very high fertility among the Hutterites. *Hum. Biol.* 25: 206–264.

Ellis, F. R., Cawley, L. P., and Lasker, G. W. 1963. Blood groups, hemoglobin types, and secretion of group-specific substance at Hacienda Cayalti, North Peru. *Hum. Biol.* 35: 26–52.

Ford, D. K., and de Mos, A. M. 1964. Serum uric acid levels of healthy Caucasian, Chinese, and Haida Indian males in British Columbia. *Canadian Med. Assoc. J.* 90: 1295–1297.

Fortes, M. 1954. A demographic field study in Ashanti. *Culture and Human Fertility.* UNESCO publication.

Fraser, A. S., Burnell, D. M., and Miller, D. 1967. Simulation of genetic systems. X. Inversion polymorphism. *J. Theoret. Biol.* (In press.)

Genovés, S. 1963. Estimation of age and mortality. In *Science in Archeology,* D. Brothwell and E. Higgs (eds.). New York: Basic Books, Inc., pp. 353–364.

Gershowitz, H., and Neel, J. V. 1965. The blood groups and secretor types in five potentially fatal diseases of Caucasian children. *Acta Genet. Stat. Med.* (Basel) 15: 261–308.

Gershowitz, H., Junqueira, P. C., Salzano, F. M., and Neel, J. V. 1967. Further studies on the Xavante Indians. III. Blood groups and ABH-Le^a secretor types in the Simões Lopes and São Marcos Xavantes. *Amer. J. Hum. Genet.* 19: 502–513.

Giles, E., Walsh, R. J., and Bradley, M. A. 1966. Micro-evolution in New Guinea: The role of genetic drift. *Ann. N. Y. Acad. Sci.* 134: 655–665.

Guerra, R., Wheby, M. S., and Bayless, T. M. 1965. Long-term antibiotic therapy in tropical sprue. *Ann. Int. Med.* 63: 619–634.

Haldane, J. B. S. 1949. Disease and evolution. Supplement. *La Ricerca Scien.* 19: 68–76.

Haldane, J. B. S. 1957. Natural selection in man. *Acta Genet. Stat. Med.* (Basel) 6: 321–332.

Hallowell, A. I. 1938. The incidence, character, and decline of polygamy among the Lake Winnipeg Cree and Saulteaux. *Amer. Anthropol.* 40: 235–256.

Hallowell, A. I. 1963. American Indians, white and black: The phenomenon of transculturalization. *Current Anthropol.* 4: 519–532.

Hamilton, H. B., Neel, J. V., Kobura, T. Y., and Ozaki, K. 1961. The frequency in Japan of carriers of the rare "recessive" gene causing acatalasemia. *J. Clin. Invest.* 40: 2199–2208.

Harris, H. 1966. Enzyme polymorphisms in man. *Proc. Roy. Soc. Lond.,* Series B, 164: 298–310.

Harrison, G. A., and Salzano, F. M. 1966. The skin color of the Caingang and Guarani Indians of Brazil. *Hum. Biol.* 38: 104–111.

Hubby, J. L., and Lewontin, R. C. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. The number of alleles at different loci in *Drosophila pseudoobscura. Genetics* 54: 577–594.

Hunt, E. E., Jr. 1950. Discussion of paper by J. B. Birdsell. *Cold Spring Harbor Symp. Quant. Biol.* 15: 314.

Jarcho, S. (ed.) 1966. *Human Palaeopathology.* New Haven: Yale University Press.

Jenness, D. 1922. The life of the copper Eskimos. *Canadian Arctic Expedition Report, XII.* Ottawa.

Keiter, F., and Salzano, F. M. 1963. Der Wachstums und Alterungsfluss (die Biorrhese) anthropologischer Merkmale an Brasilianischen Indianern. *Homo* 14: 193–217.

KENNY, J. F., BOESMAN, M. I., AND MICHAELS, R. H. 1967. Bacterial and viral coproantibodies in breast-fed infants. *Pediatrics* 39: 202–312.

KIMURA, M., AND CROW, J. F. 1964. The number of alleles that can be maintained in a finite population. *Genetics* 49: 725–738.

KING, J. L. 1967. Continuously distributed factors affecting fitness. *Genetics* 55: 483–492.

KRAUS, B. S., AND WHITE, C. B. 1956. Microevolution in a human population: A study of social endogamy and blood type distribution among the Western Apache. *Amer. Anthropol.* 58: 1017–1043.

KRZYWICKI, L. 1934. *Primitive Society and Its Vital Statistics.* London: MacMillan and Co.

LAUGHLIN, W. S. 1950. Blood groups, morphology, and population size of the Eskimos. *Cold Spring Harbor Symp. Quant. Biol.* 15: 165–173.

LAYRISSE, M., LAYRISSE, Z., GARCIA, E., AND WILBERT, J. 1962. Blood group antigens of the Pemon Indians of Venezuela. *Amer. J. Phys. Anthropol.* 20: 411–420.

LAYRISSE, M., AND WILBERT, J. 1960. *El Antigeno del Sistema Sanguineo Diego.* Caracas: Fundación Creole y Fundación Eugenio Mendoza.

LEVI-STRAUSS, C. 1944. The social and psychological aspects of chieftainship in a primitive tribe: The Nambikuara. *Trans. N. Y. Acad. Sci.* Series II. 7: 16–32.

LEVI-STRAUSS, C. 1963. *Structural Anthropology.* New York: Basic Books.

LEWONTIN, R. C., AND HUBBY, J. L. 1966. A molecular approach to the study of genic heterozygosity in natural populations. II. Amount of variation and degree of heterozygosity in natural populations in *Drosophila pseudoobscura. Genetics* 54: 595–609.

LIVINGSTONE, F. B. 1960. Natural selection, disease, and ongoing human evolution, as illustrated by the ABO blood groups. *Hum. Biol.* 32: 17–27.

LÜNING, K. G., AND SHERIDAN, W. 1966. Do recessive lethals have dominant deleterious effects in mice? *Mut. Res.* 3: 340–345.

MACCLUER, J. W., AND SCHULL, W. J. 1963. On the estimation of the frequency of nonpaternity. *Amer. J. Hum. Genet.* 15: 191–202.

MATSON, G. A., AND SWANSON, J. 1963. Distribution of hereditary blood antigens among Indians in Middle America. II. Tzotzil and other Maya. *Amer. J. Phys. Anthropol.* 21: 1–14.

MAYBURY-LEWIS, D. 1967. *Akwẽ-Shavante Society.* Oxford: Clarendon Press. 356 pp.

MILKMAN, R. D. 1967. Heterosis as a major cause of heterozygosity in nature. *Genetics* 55: 493–495.

MOTULSKY, A. G. 1960. Metabolic polymorphisms and the role of infectious diseases in human evolution. *Hum. Biol.* 32: 28–62.

MOURANT, A. E., AND KOPEČ, A. C. 1958. *The ABO Blood Groups.* Springfield: C. C Thomas.

MULLER, H. J. 1950. Our load of mutations. *Amer. J. Hum. Genet.* 2: 111–176.

NEEL, J. V., AND SALZANO, F. M. 1964. A prospectus for genetic studies of the American Indian. *Cold Spring Harbor Symp. Quant. Biol.* 29: 85–98.

NEEL, J. V., SALZANO, F. M., JUNQUEIRA, P. C., KEITER, F., AND MAYBURY-LEWIS, D. 1964. Studies on the Xavante Indians of the Brazilian Mato Grosso. *Amer. J. Human Genet.* 16: 52–140.

NEEL, J. V., MIKKELSEN, W. M., RUCKNAGEL, D. L., WEINSTEIN, E. D., AND GOYER, R. A. 1967. Further studies on the Xavante Indians. VIII. Some observations on blood, urine, and stool specimens. (Manuscript.)

NICHOLS, E. M., LEWIS, H. B. M., COOPER, D. W., AND BENNETT, J. H. 1965. Blood group and serum protein differences in some Central Australian aborigines. *Amer. J. Hum. Genet.* 17: 293–307.

NIJENHUIS, L. E., GUGTEN, A. C. VAN DER, BUTTER, H. DEN, AND DOELAND, J. W. 1966. Blood group frequencies in northern West New Guinea (West Irian). *Amer. J. Hum. Genet.* 18: 39–56.

NISWANDER, J. D. 1967. Further studies on the Xavante Indians. VII. The oral status of the Xavantes of Simões Lopes. *Amer. J. Hum. Genet.* 19: 543–553.

NISWANDER, J. D., KEITER, F., AND NEEL, J. V. 1967. Further studies on the Xavante

Indians. II. Some anthropometric, dermatoglyphic, and nonquantitative morphological traits of the Xavantes of Simões Lopes. *Amer. J. Hum. Genet.* 19:490–501.

O'Brien, W. M., Burch, T. A., and Bunim, J. J. 1966. Genetics of hyperuricemia in Blackfeet and Pima Indians. *Amer. J. Rheum. Dis.* 25: 117–119.

Osborne, R. H. 1958. Serology in physical anthropology. Technical problems as revealed by repeated blood determinations in twins. *Amer. J. Phys. Anthropol.* (n.s.) 16: 187–195.

Otten, C. 1967. On pestilence, diet, natural selection and the distribution of microbial and human blood group antigens and antibodies. *Current Anthropol.* 8: 209–226.

Platt, J. R. 1966. *The Step to Man.* New York: John Wiley and Sons.

Polunin, I., and Sneath, P. H. A. 1953. Studies of blood groups in South-East Asia. *J. Royal Anthropol. Inst.* 83: 215–251.

Post, R. H. 1962. Population differences in vision acuity: a review, with speculative notes on selection relaxation. *Eugen. Quart.* 9: 189–212.

Post, R. H. 1966. Deformed nasal septa and relaxed selection. *Eugen. Quart.* 13: 101–112.

Ride, L. T. 1934. On the anthropological aspect of blood grouping. *Caduceus* 13: 126–131.

Sabin, A. B. 1954. Genetic factors affecting susceptibility and resistance to virus diseases of the nervous system. In *Genetics and the Inheritance of Integrated Neurological and Psychiatric Patterns,* D. Hooker and C. C. Hare (eds.). Baltimore: Williams and Wilkins, pp. 57–66.

Salzano, F. M. 1961a. Studies on the Caingang Indians. I. Demography. *Hum. Biol.* 33: 110–130.

Salzano, F. M. 1961b. Studies on the Caingang Indians. III. Blood groups. *Amer. J. Phys. Anthropol.* 19: 391–404.

Salzano, F. M. 1964. Demographic studies on Indians from Santa Catarina, Brazil. *Acta Genet. Med. Gemel.* 13: 278–294.

Salzano, F. M., Neel, J. V., and Maybury-Lewis, D. 1967. Further studies on the Xavante Indians. I. Demographic data on two additional villages: Genetic structure of the tribe. *Amer. J. Hum. Genet.* 19: 463–489.

Schull, W. J. (ed.) 1963. *Genetic Selection in Man.* Ann Arbor: University of Michigan Press.

Schull, W. J., and Neel, J. V. 1965. *The Effects of Inbreeding on Japanese Children.* New York: Harper and Row.

Shreffler, D. C., and Steinberg, A. G. 1967. Further studies on the Xavante Indians. IV. Serum protein groups and the SC_1 trait of saliva in the Simões Lopes and São Marcos Xavantes. *Amer. J. Hum. Genet.* 19: 514–523.

Simmons, R. T., Graydon, J. J., Champness, L. T., and Gajdusek, D. C. 1964. Blood group gene frequencies in natives of Cape Gloucester, Western New Britain, and the Gazelle Peninsula, Eastern New Britain. *Amer. J. Phys. Anthropol.* 22: 5–14.

Simmons, R. T., Graydon, J. J., Gajdusek, D. C., Schofield, F. D., and Parkinson, A. D. 1965. Blood group genetic data from the Maprik area of the Sepik District, New Guinea. *Oceania* 35: 218–232.

Simmons, R. T., Tindale, N. B., and Birdsell, J. B. 1962. A blood group genetical survey in Australian aborigines of Bentinick, Morington and Forsyth Islands, Gulf of Carpentaria. *Amer. J. Phys. Anthropol.* 20: 303–320.

Sved, J. A., Reed, T. E., and Bodmer, W. F. 1967. The number of balanced polymorphisms that can be maintained in a natural population. *Genetics* 55: 469–481.

Tashian, R. E., Brewer, G. J., Lehman, H., Davies, D. A., and Rucknagel, D. L. 1967. Further studies on the Xavante Indians. V. Genetic variability in some serum and erythrocyte enzymes, hemoglobin, and the urinary excretion of β-aminoisobutyric acid. *Amer. J. Hum. Genet.* 19: 524–531.

Turnbull, C. M. 1965. *Wayward Servants.* New York: Natural History Press.

Vallois, H. V. 1937. La durée de la vie chez l'homme fossile. *Anthropologie* 47: 499–532.

Vallois, H. V. 1960. Vital statistics in prehistoric populations as determined from archeological data. In *The Application of Quantitative Methods in Archeology,* R. F. Heizer and J. F. Cook (eds.). Viking Fund Publications in Anthropology No. 28, pp. 181–222.

VOGEL, F., PETTENKOFFER, H. J., AND HELMBOLD, W. 1960. Über die Populations genetiks der ABO-Blutgruppen. *Acta Genet. Stat. Med.* (Basel) 10: 267–294.

WAHLUND, S. 1928. Zusammensetzung von Populationen und Korrelations erscheinungen von Standpunkt der Vererbungslehre aus betrachtet. *Hereditas* 2: 65–106.

WALLACE, B. 1965. The viability effects of spontaneous mutations in *Drosophila melanogaster*. *Amer. Naturalist* 99: 335–348.

WEBSTER, L. T. 1932. Experimental epidemiology. *Harvey Lect.* 27: 154–178.

WRIGHT, S. 1931. Evolution in Mendelian populations. *Genetics* 16: 97–159.

WRIGHT, S. 1966. Polyallelic random drift in relation to evolution. *Proc. Nat. Acad. Sci.* (U. S.) 55: 1074–1081.

WYNNE-EDWARDS, V. C. 1962. *Animal Dispersion in Relation to Social Behavior.* Hafner: New York.

YASUDA, M. 1966. *The Genetical Structure of Northeastern Brazil.* Ph.D. Thesis, The University of Hawaii.