

The Genetic Structure of a Tribal Population, the Yanomama Indians

XII. BIODEMOGRAPHIC STUDIES¹

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ABSTRACT The Yanomama Indians of Southern Venezuela and Northern Brazil are one of the largest, relatively unacculturated tribes of the tropical rain forest. Over a period of eight years data have been collected from a considerable portion of their territory on estimated age, sex ratio, fertility rates (as determined by physical examination and urine tests), and infant death rates. Although it has been impossible to collect direct data on infanticide, this subject can be approached indirectly through distortions of the sex ratio and anecdotal information. Some historical data are also available as a basis for estimating tribal expansion in the past 100 years. With this material it has been possible to construct Life Tables for the Yanomama, and to explore the results of various perturbations of the input parameters.

Data are also presented on patterns of mating and reproduction: number of spouses, mean and variance in number of surviving children, frequency of "extra-marital conceptions" based on the results of extensive blood group typings, and consanguinity rates as determined by observation and computer simulation.

Although we do not present the Yanomama as typical, these data are seen as providing a basis for more realistic population models than have existed in the past. In addition, the data provide a basis for relatively precise estimates of such demographic measures as Fisher's Reproductive Value, Crow's Index of Total Selection, and Weiss' Index of Growth Regulation.

Most of our concepts and models of the genetic structure of human populations are understandably strongly influenced by demographic studies of civilized groups. In fact, however, human genetic differences and polymorphisms came into existence under very different circumstances, while man was sustained by hunting-and-gathering and/or simple agriculture, and aggregated into bands or "villages" rather loosely organized as a tribe. Our knowledge of the demographic structure of such groups is woefully inadequate. The present paper will attempt to assemble a series of observations on the Yanomama Indians of Northern Brazil and Southern Venezuela in such a way that a reasonably complete description of the vital statistics of a largely unacculturated group will emerge. Hopefully, the parameters we will

define will be helpful in the formulation of models of the population structure of man during prehistoric times. No effort will be made in this presentation at a comprehensive review of the voluminous but fragmentary anthropological literature on this subject.

The Yanomama Indians currently occupy an area in northern South America of about 100,000 square miles, bounded approximately by latitudes 0°–5° North

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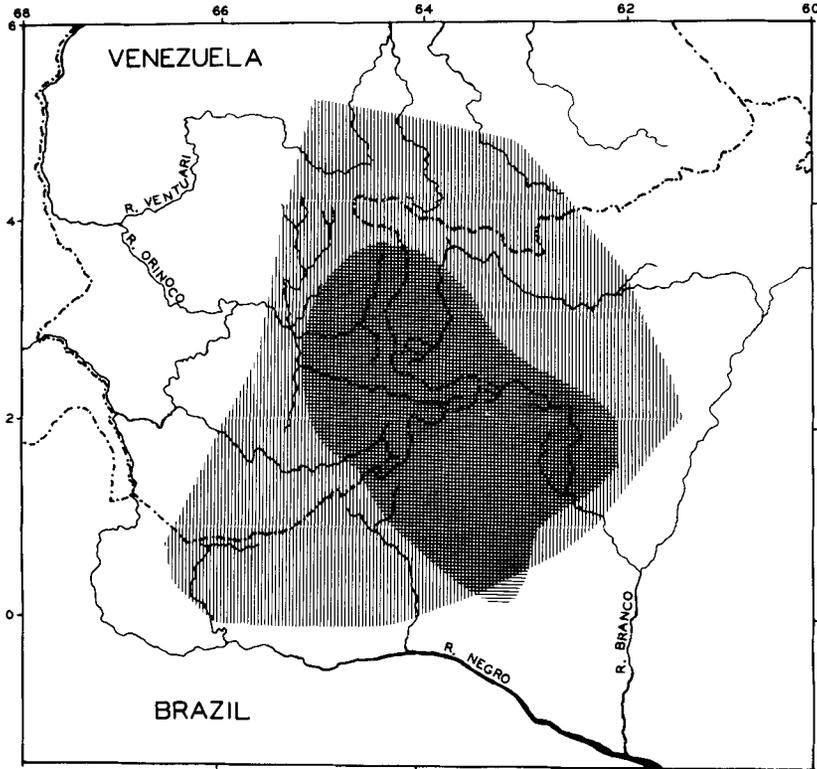


Fig. 1 The present-day distribution of the Yanomama. The central area corresponds to their approximate distribution one hundred years ago.

and longitudes of 61° – $66^{\circ}30''$ West (fig. 1). Although encountered by some of the early explorers of this region, sustained contacts of any of their villages with non-Indians seem first to have begun in the early 1950's; by our best current estimate there are approximately 15,000 Yanomama distributed amongst 125–150 villages, some still uncontacted [Migliazza ('72) believes the number of villages may be as high as 200]. They are thus one of the largest relatively unacculturated tribes of the tropical rain forest in South America. Their culture and language have been described, *inter alia*, by Becher ('60), Zerries ('64), Migliazza ('66, '67, '72) and Chagnon ('68, '74). They have also been subjected to extensive genetic, anthropometric, and dermatoglyphic characterizations (review in Neel, '70; Neel et al., '72).

The recency of contact and size of the population was thought to render the Yanomama unusually favorable subjects for the study of the demography of primi-

tive man. On the other hand, it seems clear that even prior to physical contact with non-Indians they were being influenced in a variety of ways by post-Columbian developments (cf. Neel, '72). Especially significant are the probable introduction from the Old World of falciparum malaria and the cooking banana; the Yanomama now depend on the latter for 60–70% of their calories. We also suspect that even their limited contacts with non-Indians may have already introduced some demographic changes (see below). Thus we do not claim that our findings can be equated to Amerindian demography prior to the discovery of the New World, nor can they be equated in detail to any other tribal group where different environmental circumstances would have at least some demographic effect. We do believe, however, that the general demographic character of the Yanomama is representative of that of primitive man.

Our field work among the Yanomama

first began in 1964 and has continued to the present time. As will become apparent, a considerable portion of the anamnestic data was collected by Dr. Napoleon Chagnon, to whom we are most grateful, and in whose writings are found adequate descriptions of the state of acculturation of, and the problems in collecting such data among, the Yanomama (Chagnon, '68, '74). A substantial fraction of the villages from which the data to be reported emanate have in the past 20 years established fleeting or semi-permanent contacts with small mission posts (usually staffed by one or two couples), employees of the governmental health services, scientists, or visitors. It is impossible to appraise the influence of those presences on the data presented herein, but it could take three principal forms: (1) a decrease in abortion and infanticide due primarily to the efforts of the missionaries to discourage these practices, (2) a decrease in infant and childhood mortality due to the introduction of a limited supply of antibiotics by missionaries and health personnel, and (3) a rise in mortality rates, primarily among the young, due to the introduction into some villages of alien infectious diseases such as respiratory diseases or measles (Neel et al., '70). There is no entirely satisfactory way to evaluate these possibilities. Undoubtedly the missionary presence has saved several infants from infanticide; on the other hand, the Yanomama have been quite resistant to missionary teachings. Furthermore, it is customary for entire villages to go off on hunting-and-gathering treks or visits to remote villages, where there is no contact with non-Indians, and no interference with the natural course of disease. The missionary supply of effective antibiotics is usually intermittent. In summary, while we cannot deny some impact of recent non-Indian influences on the data to be presented, we believe it to be minimal.

There is of course the possibility of significant local differences in the vital phenomena to be described in this paper, as well as, given the time span of data collection, temporal heterogeneity. Our data are inadequate for a critical exploration of these questions, which are standard to efforts to treat the demography of groups of this nature. Accordingly, in deriving

various parameters we shall regularly pool data from all the areas we have sampled. Hopefully, with the acquisition of further information it will be possible to determine whether the interplay of the vital phenomena to be described later varies from area to area.

THE BIRTH, DEATH AND GROWTH RATES

The Yanomama census. Data are available from 29 Yanomama villages. Figure 2 presents the census as a histogram of enumerations of 5-year age classes. Since the collection of the census data extended over a period of several years, there is an element of approximation in the histogram. Minor discrepancies between this histogram and one published by Chagnon ('72) are due to his updating of certain villages. Note that although the groups are small by national standards they do include over 1400 males and nearly 1200 females, which makes this one of the largest censuses ever taken among such a relatively unacculturated group over a short time period.

The Yanomama have no calendar or counting system, and therefore the gathering of age data and other historical demographic information is difficult. In the field work of our group it has been customary for individuals engaged in specific functions (physical examinations, anthropometric measurements, ethnographic studies) to make independent estimates of age, and reasonable agreement has been observed, the most signal discrepancies arising in the case of "older" women. The difficulty in collecting accurate demographic data is compounded by the reluctance of the Yanomama to answer anthropologists' questions with candor, or to speak of the deceased, a situation discussed thoroughly by Chagnon ('68, '74). These facts of course render the age pyramid more approximate than in a society with adequate birth records. All this notwithstanding, several important points may be gleaned from the age pyramids in figure 2. First, there is a great excess of males among children. Second, the male pyramid ascends rather smoothly, as would be expected for a stable population (see below), while the female age pyramid is noticeably irregular between ages

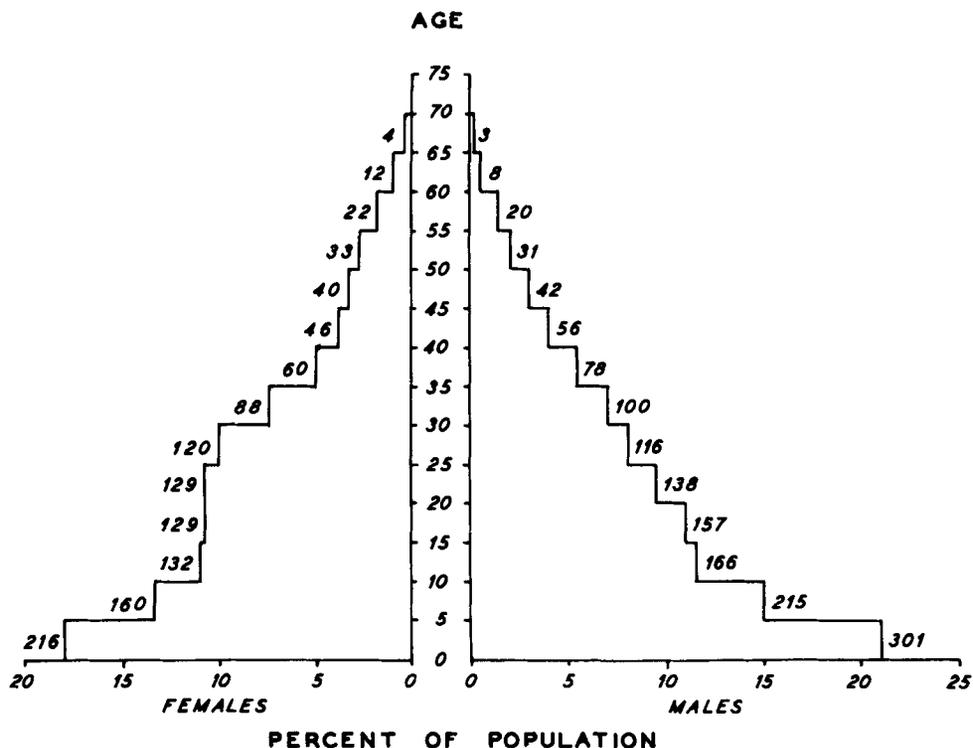


Fig. 2 The Yanomama age pyramid.

10 and 40. Third, there are very few individuals alive who are over age 60. Fourth, the number of young juveniles is very large compared to the number of young adults, indicating a pattern of high juvenile mortality, or a recent increase in births.

The female age pyramid has an apparent bulge between ages 15 and 30. This can be explained in only two general ways. Either there was a demographic change of some sort in the past, or there are errors in the estimates of age which create an artificial bulge in the pyramid. If there has been such a change, it was of a sort which persisted about 15 years, followed by a reversion to former conditions, and it was one which did not affect males, for the bulge does not appear in the male side of the age pyramid. A deficit in females in any age class could be explained by a temporary imposition of increased mortality to those cohorts, such as increased female infanticide. It is more difficult to explain an excess of females, however,

since in all properly studied human societies, males are born in greater numbers than females, and since the Yanomama practice selective female infanticide.

It seems more likely that the female age pyramid is disturbed by aging errors than by sporadic events, a finding in common with many other anthropological demographic studies. Howell ('71) notes the widespread under-reporting of individuals in the 10-14 age class in many studies, and this general topic is discussed in the United Nations publication on demographic estimation ('67). McArthur ('72) has described this phenomenon among censuses of the Fore of New Guinea and cites similar findings by van de Kaa. *Falciparum* malaria seems to have reached some of the Yanomama villages in the past 20 years, and this has been suggested as a cause of irregularity in the age pyramid for four villages (MacCluer et al., '71); however, this irregularity now seems to appear only in the female half of the age pyramid, and we must attribute the same

irregularity in the whole 29-village census primarily to difficulty in assessing the ages of fertile-age females who had young children, wherein the youngest such women were assumed to be in their 20's and the older ones to be in their early 30's. The male and female age pyramids seem to have very similar slopes except for the bulge just discussed and, since the slope is related to mortality rates, this indicates that the general mortality levels for both sexes are similar.

The results of physical examinations for pregnancy. A total of 277 women between an estimated age of 15 and 44, from 19 different villages, have been examined for the presence of a uterus at or above the level of the umbilicus. Of these, 138 were examined during 1966 and 1967 in connection with an attempt at complete physical examinations of all the members of 13 Yanomama villages located in Venezuela and Brazil. These villages in general had experienced more contact with small mission posts than those contacted later in the field work. An additional 139 women were scored for a uterus of this size in six Venezuelan villages in 1968, 1969, and 1970, in an examination limited to the abdomen.

All ages were estimated by the examiner. The problems of estimating age in a population which has no counting system nor calendar have already been mentioned. The estimation of the frequency of pregnancy is restricted to women judged to be in the age of reproduction. In the case of pubertal girls, it was customary to ask if they had undergone the puberty ceremony, more or less synonymous with the menarche. We did not in the course of our systematic examinations encounter any pregnant women below an estimated age of 15, and so do not tabulate a 10-14 age interval.

However, in a village in which it was not possible to carry out pregnancy examinations, we encountered one mother with a 6-months baby, whose age was estimated as not more than 14. Our pregnancy rates are thus limited to women age 15 or greater. At the other end of the age scale, the data on women over age 40 are limited to women of this estimated age who stated they were still menstruating.

An effort was made to include all of the potentially pregnant women of a village in the examinations. However, it was not uncommon for some women to be absent from the village at the time of the examination. Furthermore, in some of the more remote villages, some of the women refused examination, from distrust or fear of strangers. However, we are not aware of any tendency for pregnant women to avoid examination disproportionately. The uterus usually reaches the umbilicus between the completion of the fifth and sixth lunar month. It is thus at or above this level during $\frac{4}{10} - \frac{5}{10}$ of a 10 lunar month pregnancy. With 13 lunar months in a year, the proportion of women pregnant each year is calculated as

$$\frac{\text{number with uterus above umbilicus}}{\text{total examined}} \times \frac{10}{4.5} \times \frac{13}{10}$$

Table 1 presents the observed frequency of pregnancy by 5-year age intervals. Twenty-seven women were pregnant by these criteria, a crude ratio of pregnancy of 0.28; weighting the age-specific rates by the proportions of women in each age class in the entire census (sampling problems led to their not being tested in these proportions), we get an average Gross Pregnancy Rate of 0.250 per woman per year. We assume *a fortiori* that these represent the annual rates of production in a stable demographic setting.

TABLE 1

The results of physical examinations and urine tests for pregnancy, by five-year age groups

	Estimated age							Total
	15-19	20-24	25-29	30-34	35-39	40-44	45+	
Number of examinations	67	56	61	45	32	13	3	277
Positive	4	4	9	6	3	1	0	27
Number of urines tested	70	59	66	52	34	13	7	301
Positive	18	12	12	11	3	3	2	61

Urine specimens from 14 of the 27 women scored as pregnant by this approach were tested for the occurrence of increased amounts of chorionic gonadotropins (see below). In 11 instances, the test was positive. The three women with negative tests had uteri recorded as 4, 5, and 10 cm above the umbilicus. Under field circumstances, there was no possibility of supervised urine collections. Since a small gift was involved, there was some incentive to the women to present a urine specimen, but no commitment on her part that it be her own specimen (despite instructions). Accordingly, we find it difficult to decide the relative importance in these discrepancies of physiological factors (see next section), sample substitutions, and loss of activity under difficult transport and storage conditions.

The results of urine tests for pregnancy. In the field work of 1968, 1969, 1970, and 1971, "spot" urine specimens were obtained in as many villages as possible (17 from women judged to be in the age of reproduction (by the previously enunciated criteria). The presence of urinary chorionic gonadotropins was routinely determined by the hemagglutination inhibition test (Wampole UCG test); positive tests were accepted only if confirmed by the rat bioassay method. In the collection of 1969, a second hemagglutination inhibition test was employed (The Pregnosticon Test of Organon), and in 1970 and 1971, the rat bioassay method was routine rather than only confirmatory. (We are grateful to Dr. Uwe Goebelsmann for his enthusiastic cooperation in the performance of these tests).

The results are shown in table 1. Sixty-one of the 301 tests were positive. This test usually becomes positive at the beginning of the second month of pregnancy and remains so thereafter. However, the titer in international units (IU) of urinary chorionic gonadotropins, after reaching a high of approximately 500,000 IU/24 hours at the 60-70th days of gestation, falls rapidly, and is maintained at about 8,000 IU/24 hours thereafter. Although most obstetrical laboratories know that this test may be negative in the later stages of pregnancy, we have not found any precise study of the frequency of this event. If we accept the very scanty data of the preced-

ing section as the best available under our circumstances, then approximately 3/14 of pregnancies in the last half of gestation will yield negative tests, resulting in a correction of $(14 + 14)/(14 + 11) = 28/25$ per pregnancy detected. Obviously this is a poor "correction factor," but all we have. Thus the gross pregnancy rate based on the urine test becomes

$$\frac{61}{301} \times \frac{10}{9} \times \frac{28}{25} \times \frac{13}{10} = 0.33,$$

or, a pregnancy every three years. The age-distribution-weighted average here is 0.290 pregnancies per woman per year.

As noted, females from 19 villages were included in the physical examinations, and from 17 villages in the urine tests. The latter villages are not a subset of the former. Thus, in 1966, physical examinations were performed in four villages in which urine tests for pregnancy were not obtained. At the beginning of the program, we worked the easier villages, namely, those with considerable contact with missions, and this was true of these four. Our later field work took us into the more remote parts of Yanomama-land. Thus, the physical examinations were in general on Indians with more contact with missions than were the urine tests.

The frequency of abortion and infanticide. The Yanomama are known to practice both abortion and infanticide. However, this is a subject they do not freely discuss, and although both our anthropological and missionary colleagues have abundant anecdotal evidence, systematic data do not exist. All informants agree that infanticide is more often directed towards female than male infants, and towards the deformed of *both* sexes. Abortion, which of course is unbiased with respect to sex of infant, is precipitated by direct trauma to the abdomen, with rupture of the fetal membranes. Since this is not a very effective method until the uterus is well above the pelvic brim, abortions occur rather late in pregnancy. Although we have no direct evidence on the point, we suspect that some abortions occur after the uterus has reached the umbilicus, so that in computing livebirth rates from the results of urine tests or physical examination, one must reckon that some fraction of these pregnancies will yet be terminated by abortion. On the basis of the frequency of anec-

notes concerning abortions, we estimate that 5–10% of pregnancies are terminated in this fashion.

A minimal estimate of the frequency of infanticide may be drawn from the discrepancy between the number of males and females during the first two years of life. We will assume the usual male:female ratio at birth of approximately 105:100. Among the Yanomama, the observed ratio of males to females during the first two years is 140:100. This could be brought about by the killing of about 25% of live-born females. On the basis of our anecdotal data, we estimate that 5% of all infants, regardless of sex, are killed for reasons other than sex (e.g., insufficient child spacing, deformity). This requires that 30% of all female infants and 5% of males would be killed in total. We will assume that about 15 to 20% of *all* pregnancies are followed by infanticide, and the results of these, as well as abortions and stillbirths, may not be reported in the reproductive history of the mother. Then an approximate estimate of the "effective birth rate" *per adult woman* for liveborn infants permitted to live can be obtained by multiplying the figure previously obtained by 0.85. The average of the [weighted] gross pregnancy rates from observation is 0.27, a birth about every 3½ years; the "effective birth rate" becomes 0.23, a birth every four years.

The observations of "outsiders" on live-birth frequency. There are available three small data sets on frequency of livebirths among the Yanomama:

(1) Miss Sue Albright, missionary, relates that on the basis of records which she hopes are complete, between 1959 (the year contacts were established) and 1966, there were 42 births in the village of Borabuk, on the Mucujai River in Brazil. During this period, the average number of fertile women in the village each year was estimated at 18. This amounts to a live birth every three years. She is aware during this period of six abortions, five of them induced, all terminating in a still birth. There was no infanticide (were some of the abortions concealed infanticide?), but she relates two instances where but for the missionary presence, the child would probably have been killed.

(2) Mr. and Mrs. Rodney Lewis, mis-

sionaries, relate that on the basis of their records, again as complete as they could keep, between 1959 (the year contacts were established) and 1966 there were 49 births (one resulting in twins) in the village of Parimtedi, on the Uraricoera River in Brazil. During this period, there were on the average 21 women in the village estimated to be in the child-bearing age. This is a livebirth every 3.3 years. They were aware of no induced abortions during this period, but five of these infants were killed immediately after birth.

(3) Dr. Napoleon Chagnon, subsequent to a 1965 census of four villages located near the confluence of the Mavaca and Orinoco Rivers in Venezuela (the Namoweitedi), attempted to obtain a complete record of all infants born during 1966 and 1967. During those two years, there was one birth to a woman in the age interval 10–14 (26 woman-years-at-risk-of-pregnancy involved), 62 to women aged 15–40 (226 risk years involved) and 0 to women >40 (67 risk years involved). For the women aged 15–40, the overall frequency of livebirths (1 per 3.6 years) accords well with the other findings thus far recorded.

Given the roughness of the data and the imprecision of estimation, it was to us surprising how well the evidence converges to suggest that the average Yanomama woman in the child-bearing age *completes* a pregnancy about every 3 to 4 years, with approximately 85% of these pregnancies terminating in a liveborn child permitted to live. Unfortunately, our data do not allow us to state the usual reproductive span with accuracy. As noted, we believe reproduction is rare before the age of 15. The real problem is with setting an average age for the menopause. Indian women appear to age rapidly in their 30's and 40's, and there may be a tendency to overestimate their age. Although precise figures were not kept, when urine cups were distributed a high proportion of the women in the estimated 40–49 age bracket stated they were no longer menstruating. This impression is partially confirmed by the contrast between the number tested in the 30–39 and 40–49 age brackets and the proportions in the age brackets in the age pyramid (see below) and by the low fertility recorded by Chagnon for women over an estimated age of 40. Accordingly,

we suspect most Yanomama women enter the menopause at about the age of 40, rather than the age of 45–50 which characterizes most civilized women.

Infant and childhood mortality. Whereas objective and reliable data on the frequency of pregnancy, not biased by concealment of past births or by incomplete recall, can be collected by survey methods such as have been described, the same is not true for data on infant and childhood mortality. Accurate objective data on this subject require repeated observations of the same stable group. There are two small sets of data which meet these requirements, both made available to us by missionaries who recorded the fate of children born over a 7–8 year period in two small Indian villages. These data are adequate for rough estimates of neonatal and infant mortality, but of course can only partially account for childhood mortality (age 1–14 years). The findings are shown in table 2. While the data are so fragmentary that no statistical analysis seems warranted, several points seem worthy of comment. Firstly, the apparent absence of infanticide in Mucujai may well be due to concealment of the fact, relatively easy since birth (and infanticide, if practiced) usually occurs in the forest, away from the village. Secondly, we wonder to what extent the reported stillbirths are actually the result of infanticide or of abortion induced late in pregnancy. Thirdly, the reported frequency of death from natural causes during infancy is sufficiently higher in Waica (28%) than Mucujai (12%) to make one suspicious of heterogeneity in the data. Be this as it may, the data from the two villages suggest that of pregnancies going to term, at least 25% of the resulting infants are stillborn or the infants die of natural causes during the early years of life. From these data we would suggest that by an expected age of 15 some 30% of the prod-

ucts of term pregnancies will have died of natural causes with, of course, a very large error of estimate.

Neel and Chagnon ('68), on the basis of reproductive histories collected in four villages from women who had completed the reproductive period, recorded an average of 3.8 births, with 3.2 children surviving at the time the data were collected. The estimate of infant and childhood mortality was thus 18%, but this was minimal, since some of the living children were still quite young, and a fraction of these might be expected to die before reaching maturity. The data of the foregoing section suggest there was gross underreporting of pregnancies. We will later demonstrate that a completed fertility, to women past menopause, of about 8.2 offspring will predict the number of survivors quite well. This suggests the "average" woman failed to report 1 or 2 children subjected to infanticide and 2–4 children dying of natural causes. Accordingly, the data of this and the previous section indicate that as surmised at the time, we have earlier underestimated infant and childhood mortality *from natural causes*, and that a better estimate would be at least 30%. We will shortly contrast this revised estimate with what an analysis of the age pyramid suggests; it is clear that the nature of the data force us to make use of piecemeal inference regarding juvenile mortality.

Determining a fertility rate schedule. The pregnancy data from the urinalyses and uterine palpations (table 1) can now be used to construct (1) an age-specific fertility schedule, and (2) a schedule of *relative* age-specific fertility rates, which will be used later. The data from the two sets of pregnancy observations are shown in table 3. The rates have been corrected for fractions of undetected pregnancies, as discussed in connection with table 1, and divided by 2.05 to produce the rate at which

TABLE 2

The fate of infants born over a 7–8 year period in two small Indian villages

Village	Number of children born	Stillbirths	Infant deaths		Deaths after first year
			Infanticide	Natural	
Mucujai	42	2	0	4	1
Waica	53 ¹	2	5	10	5

¹ Includes two sets of twins.

TABLE 3

An estimation of fertility rates by age group on the basis of physical examinations and urine tests ¹

Age class	15-19	20-24	25-29	30-34	35-39	40-49
Palpation rates	0.084	0.100	0.208	0.188	0.132	0.019
Urine test rates	0.203	0.160	0.144	0.167	0.069	0.043
Average of tests	0.144	0.130	0.176	0.178	0.100	0.031 ²
Relative coefficients ($k(x)$)	1.28	1.15	1.56	1.58	0.886	0.275

¹ Rates are for daughters only, assuming sex ratio at birth of 105:100, and corrected for undetected pregnancies.

² Rate is adjusted to 0.218 of raw rate to account for menopausal women not tested (see text).

daughters only are born, assuming a sex ratio at birth of 1.05 males per female, the world average human rate which we use in the absence of our own data. Expressing fertility in terms of daughters only is a needed demographic convention for our methods.

The data in age classes 40-44 and 45-49 have been pooled to increase sample size. Earlier we noted that of women aged over 40 only those who had not reached menopause were tested for pregnancy. We therefore need to correct the data at these older ages for the total number of women who were not tested, since they should be included in computations of the average rate of bearing children for all women in the population at those ages. The number of women tested over age 40 is only 21.8% of what it should be, relative to the number of women tested in the earlier age classes, if the population were censused in proportion to the age distribution. This means that only about 22% of women over an estimated age 40 were still menstruating. The fertility rates for women over age 40 have been corrected to account for this underenumeration in those actually tested. We have averaged the rates from both sets of tests; line 3 of table 3 shows the resultant average age-specific fertility schedule for the Yanomama. It should be noted that these are annual rates for females in the various 5-year age classes.

To construct a schedule of relative age-specific fertility, we follow Weiss ('73a, '73b) in averaging the 5-year fertility rates for the seven fertile age classes (using the same value for the last two classes), and then express each age-specific rate as its fraction of the average. These relative rates, denoted by $k(x)$ for the x th class,

will be used later in fitting model age distributions to the census; they are given in table 3.

The relative age-specific fertility rates represent the pattern which fertility takes in these data. Generally, human fertility rises rapidly from age 15 to age 30, and then tapers gradually to a very low level by age 50. In our data we have a somewhat irregular pattern, where, for example, fertility appears lower in age group 20-24 than 15-19. We also have used the same rate for both age classes over 40. These irregularities may reflect real behavior, but probably are artifacts of sampling. We have no way to determine this in detail, and, rather than smoothing our observations to some prior pattern, we will use the actual rates as shown in table 3. We note in doing so that: (1) the irregularities are small and any reasonable adjustment or change in them will make little difference, (2) in fitting models to the data, the actual rates by age are unimportant so long as all women and all pregnancies are accounted for, and therefore any changes in the age pattern of fertility would affect only the apportionment of fertility by age and not the total reproduction, and (3) the error introduced by averaging fertility in the last two age classes will change overall fertility by minimal amounts only since the rates are so low.

The population growth rate. There is strong evidence that at least some of the groups censused have experienced a positive growth rate over the last century. On the basis of data in Migliazza ('72) (also Neel et al., '72), the area presently occupied by the Yanomama is approximately 2.8 times greater than it was a century ago. Migliazza ('72) has also mapped the location of all Yanomama villages, as best

as can be done, as of about 1970. From this map, and the areas of occupation a century ago and today, another growth estimate can be obtained. There are 54 villages or "village complexes" now extant in the core area occupied by the Yanomama since at least 100 years ago, and a total of 112 such villages or groupings in all of present Yanomama-land. This is an increase in village number by a factor of 2.08. It is possible that the density of villages has changed, along with their numbers and overall area (discussion in Chagnon, '73, for a portion of the Yanomama territory). In Migliazza's map, the density today in the area occupied a century ago is greater than is the overall present Yanomama density. If we assumed that the core area was only as dense a century ago as the overall area is now, the expansion of village numbers per century would be by a factor of 2.3 times.

All of these estimates of expansion during the past century would produce average *annual* population growth rates of between 0.5 and 1% per year. We cannot be sure of the details, but can be confident of the range of the various growth rate estimates. Almost any tenable combination of density, area, and village composition estimates will result in a growth rate in this range.

For a small segment of the 29 villages used here, the Shamatari, Chagnon ('74) feels that there has been growth from a village of about 300 individuals 100 years ago to a total of about 2,000 individuals in several villages today. This would require about 2% growth annually. In this treatment we prefer the lower growth rates discussed above, which are based on a consideration of the *total* tribe. This of course does not exclude significant local variations in growth rate during the past century ranging from say, 0.5 to 2%; as noted earlier, the data are inadequate for a consideration of this question.

LIFE TABLES

With a census, an estimated range for the growth rate, and a schedule of age-specific fertility, we are in a position to construct life tables for the Yanomama. We will attempt to fit "stable" population models to these data, because such models are a way of smoothing stochastic ir-

regularities in the data and because they allow us to relate males and females together into a single consistent population model. Stable population theory, the standard demographic model, is probably the best approach to data of this kind, where one is interested in the basic underlying patterns rather than the specific events of a few years, and we are further aided by the existence of a series of stable population models for anthropological populations designed for this purpose by Weiss ('73a). In that work, 72 stationary (zero growth) model life tables were derived from anthropological demographic data; also given there are a brief summary of stable population theory and methods for fitting real, nonzero growth, anthropological data to those models. We follow standard demographic practice in constructing an abridged, synthetic cohort life table for each sex and in relating the two sexes through female fertility only (a so-called "female dominant" model). This will result in a population model which is consistent with the censuses of both sexes, the growth rate, and the only available reliable fertility information, that for females. Our approach is to modify the model tables to account for clear deficits in the female juvenile census, but our methods otherwise follow those suggested by Weiss. We are, at this stage in the analysis, simply asking with which model life tables the Yanomama data are most consistent, i.e., which best *describe* the actual situation. The construction of a more comprehensive population model of course requires many more parameters, some of which we mention later.

The census counts shown in figure 1 reveal that the male age distribution is smoother, and hence more likely to represent prevailing demographic regimes, than is that for females. Further, the Yanomama practice of selective female infanticide is clearly reflected in the sex ratio among newborns. Because of this, we have been forced to consider the male age distribution as the more reliable for fitting to a stable model; once this is fitted, we can then get a better idea of underlying patterns for females.

The stationary population models were modified for various possible growth rates from 0.5 to 1% per year. Each such growth

rate resulted in 72 separate model age distributions, based on a model mortality schedule, a model growth rate, and the relative age-specific fertility schedule developed earlier and labeled $k(x)$ in table 3. Each model is determined by computing the value of \bar{f} , the average fertility rate, which would satisfy the basic renewal of stable populations:

$$1 = \sum_x e^{-rx} L_x k_x \bar{f} \quad (1)$$

where we sum over all age classes, and where r is the tested growth rate, \bar{x} is the average age in an age class, and L_x is the sum of survivorships for that class taken from each model mortality schedule: this was solved for each of the 72 model mortality schedules and for many values of r , in combination. The age distribution found from each combination of growth rate and mortality model is then given by

$$c(x) = b L_x e^{-rx} \quad (2)$$

where $c(x)$ is the percent of the population in the age class beginning with age x , and b is the crude birthrate (which is $1/\sum L_x e^{-rx}$).

The quality of fit between a model age distribution and that observed in the census is determined by summing the absolute value of the differences between observed and predicted percentages in each age class. This sum is called the Index of Dissimilarity. We tested seven growth rates at intervals between 0.5 and 1%, each with the 72 model mortality schedules, giving us over 500 model age distributions, for each sex, against which to compare the observed census. Our goal was to find a male and female age distribution, and hence growth and mortality schedules, which satisfied *all* of the following criteria: (1) the growth rate for both sexes should be the same (for internal consistency), (2) the fit of both age distributions to the census should be close, (3) the fertility rates which result from the fitted models should also be close to those observed, and (4) other aspects of the data (sex ratio, total fertility, and infanticide rates) should be consistent with the models. There is no single quantitative criterion for determining the set of model life tables best satisfying this multi-faceted goodness-of-fit test, and the tables ultimately chosen were based on

judgment as to overall consistency and fit to data.

In a fitting procedure such as this, where we are fitting equation (1) by varying its several parameters, it is clear that if one parameter is changed in value, the age distribution (equation (2)) can be kept constant by an appropriate change in other parameters. For example, as the growth rate increases, the same quality of fit is obtained with lower mortality rates, and so on. However, each such change in the parameters will affect the values of fertility, sex ratio, etc. which result from the model. Since growth and mortality rates are infinitely divisible, there is an infinity of models which will be virtually the same in the predictions which result from them. Hence it is erroneous to argue, and we do not, that slight deviations from the various vital rates modeled by us would be incorrect; rather, we can only claim to have characterized the general level of these rates among the Yanomama. We have no means of quantifying the amount of variation which could occur due to sampling errors or to real fluctuations in the vital structure of the population, however. The high consistency of our models show them to be good representations of the data available.

Prior to fitting life tables, we must try to account for the missing female infants who were the victims of preferential infanticide. It would be incorrect to construct a model which did not consider a sizeable proportion of all females born. We also have the problem of the suspected misaging of females at young ages (see earlier section on the census). We can obtain an estimate of the female juvenile mortality rates by noting that the ratio between the census in two adjacent age classes is a measure of the average survival from the central age of the first to the central age of the second age class. This survival rate is 1 minus the mortality rate between these classes. If we take the ratio of males age 5-9 to those age 0-4 in the census, and compare that to the same ratio for females, we can obtain an estimate of the relative survival rates between the sexes at these ages, not counting the victims of selective female infanticide, who are killed instantly after birth and do not appear in the census. For this age interval, the female:male ra-

tio is 1.04. Computing the same ratios for age class pairs 10-14/5-9 and for 15-19/10-14, we obtain values of 1.07 and 1.03, respectively. From these we see that, according to the data, juvenile females have about 1.05 times as great a chance of surviving as do males. We do not yet know the actual rates of survival, but the relative constancy of this figure seems to support the assertion that females are less subject to death at these ages than are males, after they have survived infancy. If we first fit the male age distribution, which we have earlier argued is more regular and less suspect of errors, we can then determine the female juvenile survival rates as 1.05 those of the males. Then we can fit an age distribution for the females which is able to account for female victims of infanticide.

We first fitted the male age distribution, and found that the best fitting distribution which would also be consistent with the female age distribution and all four fitting criterion outlined above, had a growth rate of 0.85% per year. The life tables for this age distribution and growth rate are given in table 4, and will be detailed later.

We now estimate the female juvenile survival rates by assuming that they are 1.05 times those of the males ($P(X)$ in table 4). These adjusted rates for the first four age classes in the life table, that is for ages 0, 1-4, 5-9, and 10-14, are 0.77, 0.88, 0.93

and 0.96. These are not inclusive of deaths resulting from preferential female infanticide, however, and we must correct the infant survival rate for this. In the process of fitting age distribution models satisfying the four criteria listed above, we found that female age distributions based on 55% juvenile mortality (45% survival of childhood) produced the best and most consistent fits. The chance of surviving childhood is the product of the first four survival values of the life table. In order for this project to equal 0.45, the first survival rate must be 0.57 and not 0.77. If 74% of all births survive preferential female infanticide, and these survive their first year at a rate of 0.77, then the net survival rate from birth to one year is 0.57. This means that there must be 26% female infanticide, and this is included in the mortality rates given in table 5.

Having determined the female juvenile mortality rates, we were able to select a life table, with the same growth rate as that for males, 0.85%, which was consistent with all aspects of the data. It is shown in table 5. We can indicate the quality of fit by noting first that the Index of Dissimilarity for the male age distribution was 0.10, which is indicative of a population reasonably close to stable age distribution, especially considering the nature of our data. For females, where irregularities in aging are known to distort the data, the Index was 0.13, quite low under the circum-

TABLE 4
The most satisfactory male life table for the Yanomama

Age	Q(X)	P(X)	<i>l</i> (X)	L(X)	T(X)	E(X)	C(X)
0	0.267	0.733	100	83	2147	21.5	4.6
1	0.160	0.840	73	262	2065	28.2	14.3
5	0.110	0.890	62	291	1802	29.3	15.3
10	0.088	0.912	55	262	1512	27.6	13.2
15	0.148	0.852	50	231	1250	25.0	11.2
20	0.152	0.848	43	197	1018	23.9	9.1
25	0.156	0.844	36	166	822	22.7	7.4
30	0.160	0.840	30	140	655	21.5	6.0
35	0.164	0.836	26	117	515	20.1	4.8
40	0.168	0.832	21	98	398	18.5	3.8
45	0.173	0.827	18	81	300	16.8	3.0
50	0.177	0.823	15	67	218	14.8	2.4
55	0.213	0.786	12	54	151	12.5	1.9
60	0.282	0.718	10	41	97	10.2	1.3
65	0.362	0.638	7	28	56	8.2	0.9
70	0.470	0.530	4	17	28	6.4	0.5
75	0.612	0.388	2	8	11	4.9	0.2
80 +	1.000	0.000	1	3	3	3.8	0.1

TABLE 5

The most satisfactory female life table for the Yanomama

Age	Q(X)	P(X)	l(X)	L(X)	T(X)	E(X)	F(X)	C(X)
0	0.430	0.570	100	52	1982	19.8	0.0	3.2
1	0.118	0.882	57	210	1920	33.7	0.0	12.7
5	0.066	0.934	50	243	1710	34.0	0.0	14.2
10	0.042	0.958	47	230	1467	31.2	0.0	12.8
15	0.130	0.870	45	210	1237	27.5	0.147	11.2
20	0.134	0.866	39	182	1027	26.3	0.132	9.3
25	0.137	0.863	34	158	845	24.9	0.179	7.8
30	0.140	0.860	29	136	687	23.5	0.181	6.4
35	0.143	0.857	25.2	117	551	21.9	0.101	5.3
40	0.147	0.853	21.6	100	435	20.2	0.031	4.3
45	0.150	0.850	18.4	85	335	18.2	0.031	3.5
50	0.154	0.846	15.6	72	250	16.0	0.0	2.9
55	0.188	0.812	13.2	60	178	13.4	0.0	2.3
60	0.251	0.749	10.8	47	118	11.0	0.0	1.7
65	0.327	0.673	8.1	34	71	8.8	0.0	1.2
70	0.432	0.658	5.4	21	37	6.9	0.0	0.7
75	0.570	0.430	3.1	11	16	5.2	0.0	0.4
80 +	1.000	0.000	1.3	5	5	3.8	0.0	0.2

stances. Of the models tested, the indices for males ranged from 0.41 to 0.09. For females, the range was 0.51 to 0.11. Our models were in the top 15% of all age distributions tested in regard to this Index, but were the overall best as far as the *joint fit to all data*.

We now give a brief description of tables 4 and 5. The first column is the age at the beginning of each age class; the second column is $Q(X)$, the mortality schedule or the chance that those who reach the age class will die before reaching the next age class. $P(X)$ is the chance of surviving the age class, and 1 minus $Q(X)$. $l(X)$ is the number of survivors left at the beginning of the age class out of every 100 born; $L(X)$ is the number of person-years lived in the age class per 100 born; $T(X)$ is the total number of person-years left to be lived from the beginning of the age class until all who are alive then have died. $E(X)$ is the life expectancy of those surviving to the beginning of the given age class, and is the mean number of years left to them. $F(X)$ (table 5) is the age-specific fertility rate, or the annual chance that a woman in the age class will bear a daughter. $C(X)$ is the proportion of the total population which is in the given age class, and this is the age distribution which was fitted in choosing these life tables. These are standard life table elements (Barclay, '58), although we use a slightly simplified notation for them.

We can now examine some of the characteristics of the fit of models to data. First, the age-specific fertility rates for the seven fertile age classes are:

	15-19	20-24	25-29	30-34
Observed	0.144	0.130	0.176	0.178
Model	0.147	0.132	0.179	0.181
		35-39	40-44	45-49
Observed		0.100	0.031	0.031
Model		0.101	0.031	0.031

The average pregnancy rate among all those women tested by palpation or by urines was 0.270, and that computed from the model, namely the age-specific rates weighted by the age distribution, is 0.265. The overall sex ratio of the 29 villages censused was 1.20, and the model predicts 1.15 (see below). The predicted female infanticide rate is 26%, that assumed from the data earlier was 25%. The fit is clearly an excellent one, and we can be confident that the models represent the demographic patterns underlying the Yanomama data.

We should raise a point here regarding the fertility rates. We noted in discussing the observations earlier that abortions are performed by the Yanomama; we have no detailed information on the frequency with which these actually occur. It appears that abortion is induced very late in pregnancy;

strictly speaking, our observed pregnancy rates should be discounted by the abortion rate prior to our calling them fertility rates, since the latter term refers to live births. We also do not know the rate at which male infanticide occurs (with a "balancing" amount of female infanticide in addition to that already discussed), but believe it is fairly small. Both of these factors, later abortion and infanticide beyond that implied by the sex ratio, are similar in that they involve virtually full term fetuses which are destroyed prior to appearing in an age distribution. We have no way to evaluate these two factors explicitly to model "effective fertility," so our model is such that they become a part of the value of $Q(0)$, the infant mortality rate. If we knew the rates precisely, we would adjust the years-lived-in-infancy, $L(0)$, downward to account for the fact that a certain fraction of births have zero life; the difference would be very small, however, and it must remain for future studies to examine abortion and infanticide in further detail.

We can now briefly characterize some of the basic demographic conditions of the Yanomama as a whole. The growth rate is between 0.05 and 1% annually. Infant mortality rates from natural causes are about 25%, and female infants are subjected to an initial 25% infanticide rate above what males experience. Survivorship to age 15 is about 50%, although somewhat higher in males than in females due to infanticide. In general, female mortality rates, after infanticide, are slightly lower than are those for males (which is observed generally in primitives). The life expectancy at birth is about the same for males and females, being about 20 years. For those surviving to age 15, there is an expectation of 20–30 more years of life. Between 45 and 50% of the total population is under age 15, with 7–10% over age 50.

Fertility measures show that the annual number of births per fertile female is about 0.25. The mean number of full term births for females who reach at least age 15 is 5.7, and the mean family size for those surviving beyond menopause is approximately 8.2 births; only 35% of all females who reach age 15 will live to age 50. The mean age for reproduction is 26.9 years and the generation length is 26.6 years. These fig-

ures differ because the population is growing; the generation length is the time required for a cohort of women to reproduce themselves R_0 times, where R_0 is the net reproduction rate. The net reproduction rate is 1.25, that is, each female born will on average replace herself 1.25 times. Each adult must care for 1.22 dependents. These values are all computed in a straightforward manner, using the appropriate model rates of birth and death.

The crude birth rate of the females is 0.586 and for males 0.560, and the crude death rates are 0.0501 and 0.0475. By comparison, crude birth and death rates for some modern nations are, after Keyfitz and Flieger ('68): United States, 0.021 and 0.010; Japan, 0.017 and 0.007; Fiji, 0.038 and 0.006; India, 0.041 and 0.019 (for years 1960–1965, approximately). Thus the Yanomama rates are quite high by national standards, although they are typical for primitive populations (Weiss, '73a). These figures give some gross measures of the Yanomama's general demographic experience, if they were to live under a stable condition as reflected by the available data. The life tables give much fuller detail.

The sex ratio. The overall sex ratio and the sex ratio at each age are important reflections of the mortality patterns operating in a population, and in this case can serve as checks on the population model we have fitted. Our computations have been based on an assumed 105:100 sex ratio at birth, which is about the average generally observed for humans. From our life tables, we can generate approximate age-specific sex ratios from

$$SR(x) = (1.05) \frac{Lm(x)}{Lf(x)} \quad (3)$$

Table 6 shows the predicted sex ratios; there we also list the observed sex ratios for the age classes. These are clearly erratic, due to stochastic fluctuations and other factors, and we have therefore smoothed the values graphically to arrive at a more reasonable average pattern, which is also shown. The similarity between the predicted and smoothed observed sex ratios is clear. The average ratio of predicted/observed sex ratios is 0.9992. The predicted overall ratio is 1.15 (each age class ratio weighted by $c(x)$), while the observed value is 1.20. For comparison, a

TABLE 6

A comparison of the predicted and observed sex ratios in the Yanomama (males/females)

Age class	Raw data	Smoothed graphically	Model prediction	Error ratio
0-4	139	133	134	1.008
5-9	133	130	126	0.969
10-14	127	128	119.7	0.9352
15-19	118	125	114.5	0.924
20-24	109	122	113.6	0.931
25-29	106	119	110	0.924
30-34	114	115	108	0.939
35-39	122	110	105	0.955
40-44	119	105	103	0.981
45-49	107	100	100	1.00
50-54	96	95	98	1.032
55-59	85	89	945	1.062
60-64	78	80	92	1.15
65-69	75	75	87	1.16
70-74	—	—	85	
75-79	—	—	775	
80 +	—	—	75	
Overall:	1.20		1.15	

Average error ratio (Predicted/Observed): (Under age 70) = 0.9992.

survey of 42 Amerindian populations by Salzano ('72) showed an average sex ratio of 1.093.

PATTERNS OF MATING AND REPRODUCTION

Thus far we have dealt with questions of average birth, survival, and growth rates. We now turn to a consideration of the web which connects individuals within this population. It is this nexus, together with the aforementioned vital events, which defines the breeding structure of the population. However, in this treatment one very important aspect of population structure will be left untouched, for presentation elsewhere: intervillage and intertribal migration. Ward and Neel ('70) (also Wagener, '73) have presented a preliminary treatment of this for the Makiritare, and have in preparation an extensive analysis for the Yanomama. Detailed demographic data are only available for two subdivisions of the Yanomama, a cluster of four villages called the Namowei-tedi (N) (Chagnon, '68) and a single village (Mishimishimabowei-tedi, (M)) from a subdivision called the Shamatarí (Chagnon, '74).

Number of spouses. The Yanomama are polygynous; however, their wives are not infrequently "discarded" (the term "divorce" would be inappropriate in this con-

text). More than 50% of all women who reach 15 die before menopause. While it is relatively easy to establish "wives at present," it is less easy to establish "wives ever," and to establish to what extent the wives were held simultaneously. From the genetic standpoint, however, the real point is the number of different mates by whom children are begotten. An estimate of these data for both sexes in the N and M Yanomama subdivisions is given in table 7. This is based not only on the individual's statement concerning events some years previously, but corroborated where possible. Nevertheless, given the frequency with which wives are discarded, a woman might be genuinely confused as to which husband was responsible for her impregnation; furthermore, "affairs" are common, but the question of whether a child resulted from an "affair" or from a current spouse (or from a somewhat sanctioned relationship which fits into neither of these categories) must often be moot. Male Yanomama may be no less disposed to exaggerate their attractiveness and potency than the males of other cultures. These limited data are simply presented as the best available. Three points seem valid: (1) by the time the reproductive period is completed a high proportion of both sexes will by history have achieved parenthood with multiple partners, (2) either as a result of polygyny or "affairs," men are reporting parentage by more different partners than are women, and (3) parenthood by multiple partners seems to be more common in M than in N.

Mean and variance in number of surviving children. Although the data on live-births are inadequate, the data on number of surviving children, who cannot easily be concealed in a small village, are adequate in quality if limited in quantity. Table 8 presents, for males and females separately, number of surviving offspring to those currently surviving parents at time of visit. It is noteworthy that only 1 of 40 women over 40 failed to report any surviving children, thus confirming our earlier impression of the rarity of sterility in the unacculturated Indian (Salzano et al., '67). For demographic purposes, an effort has been made to classify those individuals recently reaching adulthood by whether they were currently alive or dead, and had

TABLE 7
The number of partners by whom children begotten, in two different sets of Yanomama villages

Division	Sex	Survivorship	Number of partners by whom children produced										Number of individuals		
			0	1	2	3	4	5	6	7	8	9		10	
Namoweitedi	Males	Alive >40	8	8	5	1									22
		Dead <40	3	21	7	6	1								38
		Dead >40	1	2	4	2	1								10
	Females	Alive <40	21	36	9	2									68
		Alive >40	1	19	5	2									27
		Dead <40	9	31	4										44
Mishimishimabowetedi	Males	Dead >40	6	4											10
		Alive <40	28	56	11	4	1	1						99	
		Alive >40		2	2	2	1	1							7
	Females	Dead <40		1	2	1									4
		Dead >40		1	2	2	2								6
		Alive <40	1	16	14	2	2					1			34
Females	Alive >40		3	2	3	1								9	
	Dead <40	1	7	2										10	
	Dead >40	4	26	7	2	2								44	
														40	

survived through age 40 or not. Although an effort was made to obtain these reproductive histories for all individuals achieving maturity in these villages during the past 20 years or so, it is obviously easier to obtain these histories for the living, and the proportions in which these classes are represented cannot be taken as representative of a cohort. We note that the number of surviving children for all categories is greater for M than for N, the discrepancy being striking for males over age 40. These data tend to corroborate the data given earlier, that M men had fathered children by more women than N men. The differences for females are less striking. One way such differences could arise is by the greater accumulation of multiple wives by the senior men of M than N, which would require younger men to report fewer children, which does not seem to be the case. A second explanation could be a different age structure in the two populations, but age data for them does not support this explanation either. A third basis would be greater fertility or better newborn survival rates in M than N. Some combination of these factors, with stochastic fluctuations also involved, could be operative. The two village sets do agree on the greater variance in male fertility than in female, a finding also observed in our studies of the Xavante Indians (Salzano et al., '67).

We can compute a predicted value for the mean number of surviving children to women for any age classification from the model life tables. The number of surviving children to surviving women over age 40 is

$$x \sum_{i=40}^{80} C_j = \frac{\sum_{j=40}^{80} C_j \sum_{i=15}^j Q_i f_{i,\varphi} \bar{l}_{j-i,\varphi} + (1.05) f_{i,\varphi} \bar{l}_{j-i,\sigma}}{\sum_{k=40}^{80} C_k} \quad (4)$$

where $Q_i = 5$ for all age classes up to the last ($i = j$) and the $Q_{i=j} = 2.5$, and where \bar{l}_{j-i} is the average survivorship for the $j-i$ th age class, being the average of that at the beginning and end of that class, for the sex of child specified in the second subscript. C_j are the age-class proportions, $C(X)$, from the female life table. For women over age 40, the predicted value is 3.17 and the observed is 3.20 ± 1.65 .

Earlier we have argued that the average Yanomama woman who had completed her fertility by reaching menopause had borne

TABLE 8

Mean and standard deviation for number of surviving children, by population, sex and survivorship

Population	Sex	Survivorship	Number	Mean	Standard deviation
Namowei-tedi	Males	Alive > 40	25	3.56	2.69
		Dead < 40	27	2.19	1.62
		Dead > 40	19	5.89	3.23
	Females	Alive < 40	73	1.14	1.26
		Alive > 40	33	3.18	1.65
		Dead < 40	31	1.10	1.27
		Dead > 40	5	4.00	1.58
Mishimishi-mabowei-tedi	Males	Alive < 40	93	1.34	1.47
		Alive > 40	8	8.63	3.07
		Dead < 40	6	3.00	1.79
	Females	Dead > 40	4	7.50	4.51
		Alive < 40	24	2.33	2.79
		Alive > 40	7	3.14	2.54
		Dead < 40	10	1.50	0.97
	Dead > 40	6	5.00	1.79	
	Alive < 40	40	2.43	2.16	

about 8.24 full term births, but had failed to report several who were either killed or died of natural causes. Despite this relatively high fertility, child-spacing is also practiced. In one sense, infanticide may be viewed as an aspect of child-spacing. It would take a special study to explore thoroughly the basis for this spacing, but two readily perceived factors — not of equal importance in agricultural societies — are the prolonged dependence of the child on breast milk and the need of the women in this culture to remain highly mobile. The idea of infanticide as a spacing mechanism is well documented in earlier compendia of world-wide ethnographic data (Carr-Saunders, '22; Krzywicki, '34). The implication of a restriction in family size, especially in the minimal permissible spacing, is that the variance in progeny surviving birth would be somewhat lower, relative to the mean, than would be the case in less planned societies. Studies of civilized human societies (Brass, '58; Kojima and Kelleher, '62) generally found that the negative binomial distribution best represents the distribution of completed families in human populations and it can be shown that the distribution of progeny number will be of a less variable, Poisson form only if all women were exposed to equal risks of fertility for an equal time. Some workers (Imaizumi et al., '70) have found an approximately Poisson distribution in human data from Japan and India, and

have argued that socioeconomic homogeneity is responsible, as the Poisson law would require. This cannot be a sufficient explanation, however, since many socially homogeneous populations show a negative binomial distribution (e.g., Salzano, '63), and other factors must be involved.

In Western societies the small death toll does not materially change the distribution of surviving children (a figure not directly reported in most census summaries). With our limited data, we cannot determine variance in number of births, but we can look at the distribution of *surviving* children, who are accurately reported. We will use the data from table 8. The additive property of means and variances allows us to compute the overall mean and variance of completed family size, by summing the values for all women over 40 (who have virtually completed reproduction) and those for women who have died (thus having completed reproduction), weighted by their respective numbers. The mean of these completed families is 2.46 survivors, and the variance is 2.46, consistent with a Poisson distribution. We interpret this result as indicating that there is some effort by Yanomama mothers to regulate the size of the family of surviving children, thus reducing its variance. These calculations are for females and their issue only; table 8 shows that male reproductive performance is more variable.

"Extramartial conceptions." A child

will be classified as resulting from an "extramarital" conception if on the basis of typings for the MNSs, Rh, P, Duffy, Kidd, Lewis, Gm, Inv, and haptoglobin systems it possesses a genetic trait absent in both putative parents (the other systems studied in the Yanomama are largely monomorphic and hence of no use in this regard). These findings must be regarded with caution. First, a woman may purposely represent a child as her own. Secondly, since many women do not stay married long in this culture, there could be real doubt over which husband sired a particular child. Finally, misidentification of specimens in the field or laboratory error can result in apparent parental exclusions. The latter possibly is in part met by the fact that blood typings were performed in duplicate by two laboratories and by repeat typings on all findings resulting in apparent exclusions.

The analysis for extramarital conceptions has been restricted to the N. This is a particularly accessible group; in the course of our field trips repeat specimens have been collected from members of this group for a variety of purposes, and these have often been subject to a second, independent typing. Among a total of 132 children typed with both their parents, there were eight exclusions. The basis for these exclusions is shown in table 9. Five of the eight are two-system exclusions.

The number of exclusions may be inflated by anamnestic and laboratory errors; on the other hand, the typings will not detect all children who are extramaritally conceived. The ability of a system

to detect extramarital conceptions is a function of the number of alleles and their frequencies in the population. A truly sophisticated estimate of the efficiency of detection of non-paternity under our circumstances would also involve a separate estimate for each of the four Namoweitdi villages (because of differing gene frequencies) and allow for the frequency of consanguineous marriage and the possibility that the "other man" might be a kinsman. The scanty data do not warrant this sophistication. A rough estimate is derived by estimating the probability of exclusion for codominant systems as $pq(1 - pq)$ and for dominant systems as pq^4 , where p and q are the respective gene frequencies, and $p + q = 1$ (in systems with dominance, p is the frequency of the dominant gene) (Weiner, '31). Data are available for the following systems which are or can be treated as codominant: the M-N and S-s reactions of the MNSs complex, the C-c and E-e reactions of the Rh complex, the Hp(1) and Hp(2) proteins of the haptoglobins, the Fy(a) and Fy(b) reactions of the Duffy system, and the Gc(1) and Gc(2) proteins of the Group Component system. In addition, data are available on these reactions in systems exhibiting dominance: Jk(a) of Kidd, Inv(1) of Inv, P(1) of P, and Gm(axg)(vs gm(ag)) of the Gm system (cf. Gershowitz et al., '72; Weitkamp et al., '72; Gershowitz and Neel, in press). The compound probability of exclusion with these systems is

$$P(E) = \prod_{i=1}^n (1 - p_i q_i (1 - p_i q_i)) \prod_{r=1}^m (1 - p_r q_r^4) \quad (5)$$

where n = number of two-allele codominant systems, and
 m = number of two-allele dominant systems.

With the gene frequencies of these systems, the probability of exclusion is 0.64. The various factors mentioned above combine to render this an over-estimate. Thus, in this material about one-third of true exclusions go undetected and there should be some four instances of undetectable non-paternity in the 132 children. Accordingly, roughly 9% of children do not belong in the biological sibship to which they have been assigned.

The term "extramarital," while descrip-

TABLE 9

The basis for "parentage exclusion" for eight Yanomama children. There were no exclusions with the Hp, Fy, Gc, Jk and P systems

Individual	System resulting in exclusion				Number excluded systems
	MNSs	Rh	Gm	Inv	
03B0111		x			1
03B0207	x	x			2
03A0052			x		1
03C0300			x	x	2
08A0063	x	x			2
08C0239	x		x		2
08C0226	x	x			2
03A0020			x		1

Total number of children — 132.

tive, has somewhat different connotations for the Yanomama than for Western culture. Illicit affairs are no less resented by Yanomama husbands than by most Western husbands; however, there appear to be circumstances under which access to another man's wife is semi-sanctioned, as when one village visits another for a ceremonial feast, and men of the host village wish to be exceptionally hospitable. Understandably, nothing approaching quantitative data on the frequency of this occurrence can be obtained. Even were such data available, the frequency with which these practices result in extramarital conceptions could not be estimated, but whatever the frequency, it is encompassed in the present estimate. These data further confirm our impression of a complex web of gene transmission in the Yanomama.

Consanguinity and inbreeding. The Yanomama are not favorable material in which to study the frequency of consanguineous marriage. The fact that the population is subdivided into small semi-endogamous villages of 50–200, with a prescriptive bilateral cross-cousin marriage rule, leads to the expectation of a high coefficient of inbreeding, but this cannot be documented with accuracy because of the shallowness of the genealogies. In the complex of four N villages, 15 of 124 marriages (12%) for which one or both marital partners were alive involved full first cousins (some with additional inbreeding loops). If attention were restricted to those marriages for which all four grandparents of both partners were known, 13 of 37 (35%) involved first cousins (some again with additional loops) (MacCluer et al., '71). For the village of M, 10 of 93 marriages for which one or both marital partners were alive involved at least full first-cousins (11%) but another 14 marriages were at least half first-cousin in relationship (15%) (Chagnon, '74). A direct estimate of more remote degrees of consanguinity is impossible.

In this situation, we have resorted to a computer simulation of the Yanomama developed by MacCluer et al. ('71) to obtain insight into the coefficient of inbreeding of the average individual. In five runs of a program, whose capacity was limited to

constructing inbreeding loops for the proximal seven generations, the coefficient of inbreeding after 400 years of simulation (about 14 generations) ranged between 0.024 and 0.045, averaging 0.034, i.e., the average individual was as inbred as the child of first cousins once removed (MacCluer and Neel, unpublished). Since the coefficient of inbreeding rose between generations 6 and 7 by about the same amount as between generations 4 and 5, we surmise that the coefficient might reach 0.05 if the loops of relationship for all 14 generations could be reconstructed. However, there are aspects of the simulation, such as use of a closed population, which render this estimate tentative.

IMPLICATIONS OF RELATIONSHIPS
BETWEEN MORTALITY AND
FERTILITY SCHEDULES

We can now utilize the models of mortality and fertility to look at some aspects of their relation to each other. Three available measures which highlight these relations are presented below.

Reproductive value. Fisher ('30) derived a formula for the "Reproductive Value," by age, of members of a population. This rates the genetic or reproductive contribution to be made, on average, by a woman age x to future generations, relative to that of a neonate. It is a reflection mainly of the combined effects of past mortality and future fertility on a person's present potential to reproduce. Reproductive values for the Yanomama are shown in table 10; they are for those at the beginning age of each age class, and are computed from the following approximation to Fisher's formula:

$$v(x) = \frac{e^{rx}}{l_x} \sum_y e^{-ry} L_y f_y, \quad (6)$$

where $r = 0.0085$ and the other values are as given previously in this paper.

By definition, $v(0) = 1.0$; the other values of $v(x)$ for the Yanomama reflect the high early mortality schedule by rising sharply to a maximum of 2.52 at age 15. For comparison we also show reproductive values for Norway, with one of the world's highest life expectancies, and for Madagascar with one of the lowest life expectancies of modern nations (from Keyfitz and Flieger ('71); note that these are val-

TABLE 10

The calculation of Fisher's reproductive values (V_x) for the Yanomama and two other contemporary populations

Age	Yanomama ¹	Madagascar ²	Norway ²
0	1.0	1.28	1.041
1	1.769	—	—
5	2.074	1.601	1.099
10	2.316	1.879	1.159
15	2.524	2.007	1.171
20	2.314	1.809	0.961
25	2.073	1.390	0.582
30	1.561	0.917	0.277
35	0.956	0.478	0.099
40	0.545	0.197	0.021
45	0.045	0.062	0.001
50+	0.000	0.014	0

¹ In the Yanomama, values for v_x are those for individuals at the beginning of the age class, on their x th birthday, for females only; for Madagascar and Norway the values are average for the age class.

² From Keyfitz and Flieger, '71.

ues for the average woman in the age class rather than those at the beginning, which is of little consequence for comparative purposes). Survivorship in Madagascar to age 15 is 69% and in Norway it is 98%. Note that the restriction of family size and fertility in Norway drastically reduces $v(x)$ after age 35 or so. Reproductive value among the Yanomama is, as is always true, greatest for those who are just about to begin reproduction, but because of the differences in population structure it is more than twice as great for a Yanomama girl of 15 than a like-aged Norwegian.

Crow's index of total selection. Whereas Fisher's values represent the effects of fertility and mortality on the amount of remaining reproduction to those who have survived to various ages, another important relationship between the vital rates examines the maximum amount of selection which could occur by differential mortality and by differential fertility in the population. This is Crow's Index of Total Selection (Crow, '58), and is related to Fisher's fundamental theorem of natural selection (Cavalli-Sforza and Bodmer, '71), and hence to the maximal rate of evolution which *could* occur per generation. Crow measures the potential evolutionary effect due to variance in mortality against that due to variance in fertility; it is clear the Index measures *possible* rather than *realized* selection. Elsewhere, we have published estimates for the components of

Crow's Index for the Yanomama and several other groups (Neel and Chagnon, '68); in the light of our revised estimates of fertility rates and mortality rates, however, it is proper that we recompute them.

Given the foregoing treatment, we find it useful to approach this Index somewhat differently than Crow. The variance in total reproduction which is caused by pre-reproductive mortality is given by

$$v_m = R_0^2(1 - l_{15})/l_{15} \quad (7)$$

where R_0 is the net reproduction rate; its value is 1.25 for the Yanomama, considering females only, and the variance due to differences in fertility is

$$v_f = (1/l_{15}) \left(\sum_i p_i (\bar{x}_i - R_0/l_{15})^2 + \sum_j \sum_i (x_{ij} - \bar{x}_i)^2 \right) \quad (8)$$

where \bar{x}_i is the average fertility of those dying in the i^{th} fertile age class, and x_{ij} is the fertility of the j^{th} woman in the i^{th} class. Our formula is not the same as that given by Crow, but is merely a different way of partitioning the same variance which is useful for our demographic model. We assume that the average woman dying in the i^{th} age class has expected fertility equal to the sum of all age-specific rates prior to the i^{th} class plus 2.5 years of fertility in the class of her death. The p_i are the weights, equal to the percent of all fertile women dying in the i^{th} age class. The first term can be computed readily with the fertility rates as discussed. The second term as it appears requires a knowledge of each woman's fertility, which we do not have; it can be rewritten as

$$\sum \sum (x_{ij} - \bar{x}_i)^2 = \sum p_i v_i \quad (9)$$

where v_i is the variance in progeny for women dying in the i^{th} class. If we recall that we have shown satisfactory agreement with a Poisson distribution of number of surviving children, which we attribute to regulation of family size, we can consider that infants are killed *mainly* for reasons of spacing, and hence such infant deaths are unrelated to natural selection since their genotype is irrelevant to the cause of their deaths. We can make the assumption that the distribution of children is Poisson at each age class level, for these reasons. If this is so, then $v_i = \bar{x}_i$. From this assumption, we derive a value of $v_f = 10.43$.

From the values of v_m and v_f we compute the two components of Crow's Index

and the total index as follows: $I_m = 1.22$, $I_f = 1.36$, and $I_t = 4.24$. We find that $I_m \approx I_f$. These results constitute a considerable change in both I_m and I_f from the previously published figures. The computations here were made from our model vital rates, and hence are independent from the details of the data on which the previous figures were based. The reason for the changes are the revised mortality schedule which has greatly increased the potential for selection due to mortality, and the increased fertility when allowance is made for unreported births.

There are two aspects of Crow's Index which must be discussed in this context. Firstly, I_m is substantially inflated by infanticide (not included in the earlier calculation), which we have argued above is largely nonselective. This illustrates the need for always regarding the Index as a measure of *potential* selection. Secondly, the use of the term "fertility" for the value of I_f has a somewhat different meaning for the Yanomama than it does for modern national populations for which the Index was primarily derived; the modern-national woman has a very high chance of surviving to menopause (e.g., a Norwegian woman age 15 has a 0.97 probability of living to age 50), and therefore the distribution of progeny size among such women is determined predominantly by fertility-regulating phenomena. Among the Yanomama, only about 35% of those reaching menarche will survive to menopause, and therefore much of the variance in progeny number is due to their deaths and not merely to their failure to reproduce during their fertile period. Thus the value of I_f just derived contains some variance which is really due to mortality, and therefore we may consider that the real opportunity for selection due to mortality is even greater, relative to that due to fertility, than the figures indicate.

The index of growth regulation. A third measure of the relative effects of mortality and fertility schedules was derived by Weiss ('72, '73a) to examine population-ecological aspects of these vital rates. This is called the Index of Growth Regulation (IGR). If we have a population growing at a rate r , we can compute the rate at which that same population would grow if its mortality rates were unchanged but its

fertility were raised to the maximum sustainable human level (an hypothetical level). Call this growth rate r_f . We can similarly determine what growth rate would occur if the fertility of the observed population were unchanged but the mortality rates were lowered to their hypothetical minimum, and this would be r_m . These growth rates are determined by solving equation (1) with the requisite vital rate schedules.

The difference between the actual amount of growth and that which would occur with unchecked fertility is called fertility damping on the population, and is defined to be $r_f - r$. Mortality damping is similarly defined as $r_m - r$. The Index of Growth Regulation is

$$\text{IGR} = \frac{r_f - r}{r_m - r} \quad (10)$$

The Index weighs the relative effects of the imposition of less than maximal fertility and survivorship on the growth of the population. If fertility damping predominates in this sense, the IGR will be greater than 1.0, while if mortality damping predominates it will be less than 1.0. Generally, preagricultural populations have an IGR less than 1.0, while populations just prior to industrialization show a value very close to 1.0.

The IGR for the Yanomama is 0.738 for females (it cannot be computed for males without a fertility schedule). This means that the effect of mortality is 1.36 times that of fertility, which highlights the heavy mortality imposed on the population. We must note at this time that the fertility of the Yanomama, even before infanticide is imposed, is well below the human maximum as found among such groups as the Hutterites (Eaton and Mayer, '53), and hence that, although mortality is the predominant growth-damping influence, one cannot infer that fertility is at its maximum and undamped. Repeatedly we have shown that fertility is regulated actively among the Yanomama to limit the net progeny production of the average woman.

The demographic balance. We turn briefly to an examination of the implications of the Yanomama growth rate. We have seen evidence that for the past century the Yanomama have grown an average of 0.05 to 1% per year. This cannot

be a long-term rate, and therefore the demographic model we have built cannot be regarded as representative of aboriginal conditions in the Americas: even if only a single couple crossed the Bering Straits and became the sole progenitors of the entire Amerindian population, they would at a growth rate of 0.0085, produce 100,000-000 living descendants in only 2086 years. Since the Americas have been settled for perhaps 20,000 years, the average growth rate must have been well below this value. For instance, a uniform growth of only 0.000886 would produce 100,000,000 living descendants of an original couple after 20,000 years.

The problem of the demographic balance of animal and human populations has become an important one. For animals, Wynne-Edwards ('62) has summarized the bulk of evidence showing the behavioral means by which mortality and fertility rates, and primarily the latter, are adjusted to maintain viable population densities. Earlier, Carr-Saunders ('22) had summarized the then available data on man; not only has very little quantitative documentation been added up to now, but his ideas still stand virtually unchanged. He found that populations tended to an optimum density, and that this density can generally not be greatly exceeded by, nor is it often very much greater than, actual densities. Another notable study of this topic is that of Krzywicki ('34). Both works catalogued masses of subjective evidence on practices of infanticide, abortion, infant neglect, intercourse taboos, nutritional effects on survival and fertility, and so on. A spate of recent works deal with the ecological balance of primitive populations similarly (e.g., Birdsell, '53; Devereux, '55; Nag, '62; Rappaport, '67; Lee and DeVore, '68; Vayda, '69). The gist of all these works is to show that population homeostasis is maintained in elaborate ways which can be expressed in terms of systems theory or some similar framework. (We view the present study as a major effort to document these ecological facts of human population regulation.)

Although the average density of population in a given area probably does not change much except as culture gradually changes, there is no reason that each sub-

population in the area should be at virtual zero growth all of the time. Certainly oscillatory forces such as war, famine, disease, and so on would produce fluctuations in annual growth rates, and stochastic processes would add to this fluctuation. In general, some compensatory mechanisms will be exercised to return the group towards its optimal number. But there must also be some constant reshuffling of populations within an area, such that at any one time one subpopulation will be in numerical, territorial, and perhaps cultural ascendance while others will be in decline. Despite this flux, we can still ask what underlying vital rates characterize the *average* population in an area, and this average population will have approximately zero growth.

The Yanomama could be restored to zero growth by a rise in mortality or by a decrease in fertility, or both. A uniform increase in all mortality rates by a factor of about 1.3 would suffice, as would a reduction in all fertility to about 0.80 of its present level. An increase in infant mortality alone of 11% would reduce all adult survivorships to 80% of their present levels and would also produce ultimate zero growth. To hazard a guess as to the specific influences responsible for what must be a relatively recent increase in Yanomama growth rates from previously lower growth, we must examine the three most probable causes for that growth. First, a variety of factors could have caused a reduction in infanticide during the past 100 years, easily of the required order; such a reduction has been universally observed in primitive groups after contact, but whether contact among the Yanomama has been long or strong enough is, as we have earlier stated, doubtful. The second possible cause would be the introduction in the post-Columbian era of better food sources or technology. The final factor likely to promote growth would be the post-Columbian depopulation of lands surrounding the older Yanomama territory, providing them with room for expansion.

If we combine the effects of a slight reduction in infanticide (which has often been reported for other primitive groups to be of the order of 50%, and seems only to be about 15% currently among the Ya-

nomama), a better nutrition, and a territory into which they could and did expand, we can suggest that the growth now found among the Yanomama is a combination of effects of fertility and mortality improvements. The net result of all of these factors is probably that childhood mortality rates dropped considerably, especially among infants, but that the age-specific rates of bearing full term births and the adult mortality patterns are probably not greatly changed from aboriginal times. As is usually the case among animal populations, we suggest that adjustments in the rate of producing surviving infants are the critical factors in the growth of Yanomama populations.

DISCUSSION AND SUMMARY

This paper has attempted a clear and quantitative description of the demographic characteristics of the Yanomama population. We have taken the pooled results from study in many Yanomama villages and have derived average rates of mortality and fertility by age, and some of the consequences of those averages. We hope that these average rates will provide the basis for mathematical descriptions of primitive population structures more realistic than generally available at present, with which to explore a number of basic genetic questions as well as ethnological and demographic ones.

At this point it is fitting to discuss the nature of the descriptive model we have applied to the Yanomama. Stable population theory shows that given a set of constant fertility and mortality rates, a population reaches a stable age distribution with a growth rate "intrinsic" to those vital rates. While approaching the stable age distribution, the growth rate and ac-

tual age distribution of a projected population will differ from the stable ones to a degree which depends on the starting age distribution. Surely, also, the Yanomama growth, birth and death rates fluctuate stochastically from year to year. But we have found that the current age distributions are sufficiently close to stable ones that our models seem fair representations of the average Yanomama experience. In fact, our use of stable models served explicitly to smooth out stochastic fluctuations from the data in such a way as to reveal underlying patterns. In addition, the use of stable models has allowed us to improve a previous preliminary characterization of Yanomama demography by Neel and Chagnon ('68). Howell ('74) noted that some of the properties reported by these authors were inconsistent with each other in terms of stable populations. In this paper we have been able to correct those inconsistencies, which were based on unknown amounts of underreporting of mortality and fertility in a sample of only four villages, and to estimate the degree of some of that underreporting.

In a recent study of some six northern Yanomama villages, Ramos ('72) provides some census data. These are based on crude age breakdowns founded on social roles, but may be used for general comparison with our 29 village census. Table 11 provides these data. The overall sex ratio observed by Ramos is 1.09 whereas it is 1.20 in our larger census. The juvenile sex ratio is 1.54, while ours is 1.34. However, the female age distribution of Ramos shows fewer individuals between birth and age 15 than are between ages 15 and 30; this can only be explained generally, especially as the ages are vague, as aging error or a recent imposition of

TABLE 11

The distribution of ages in six small northern villages of the Yanomama, after Ramos ('72)

Age	Ramos		Sex ratio	29 Yanomama		Sex ratio
	M	F		M	F	
0-15	0.545	0.364	1.54	0.475	0.428	1.34
15-30 ¹	0.348	0.413		0.337	0.283	
30-50	0.072	0.132		0.116	0.195	
50+	0.035	0.091		0.074	0.094	
Overall:			1.09			1.20

¹ Ages very approximate, based on stage of life, and about 35 for males and 30 for females.

female infanticide much higher than was earlier practiced. In general, it is difficult to draw detailed conclusions about the comparison of these few villages with our census or models except that there do not seem to us to be drastic differences in the mortality patterns manifest generally by these data.

We presume that most of the important genetic characteristics of modern man arose under tribal conditions of various sorts. Some traits, such as color blindness (Neel and Post, '62), may have changed in frequency with the advent of civilization, but we must in general gear our explorations of the forces responsible for the human variability currently observed to the demographic structure of what we are calling "tribal" populations. It has not been our intent to generalize excessively from one such society, but it seems clear from this and other publications on the Yanomama that the following features of tribal society — most recognized previously — must be borne in mind in efforts to understand present-day gene frequencies:

1. Birth rates are high by contemporary national standards, but are still well below their maximum. "Reproductive compensation" for genetic deaths, which has important genetic consequences to formal treatments of the dynamics of gene frequency (discussion in Motulsky et al., '71; Schull and Neel, '72), could be a long-standing phenomenon.

2. Sterility is rare. This, coupled with the Poisson distribution in the number of surviving children, implies a more even contribution of Yanomama women to the next generation than is true of their civilized counterparts.

3. Infant and childhood mortality, including infanticide, is about 50%.

4. Continued high mortality exists throughout the reproductive period.

5. Coefficients of inbreeding may approach 0.05.

6. As a result of polygamy, "extramarital conceptions," and marital instability, approximately 50% of Yanomama reaching the reproductive age have children by more than one partner.

As a result of studies not treated in this paper, two additional characteristics of Yanomama population structure should be mentioned:

7. Relatively large genetic differences exist between demes (villages), in consequence of deme fissioning among lineal lines (Neel and Ward, '70).

8. Endogamy patterns produce a series of barriers to gene flow (village, village-clusters, tribe: a *nested* structure of population units).

In reviewing these facts about primitive societies, we feel that the chief gap in knowledge now is the cause of mortality among them, especially among adults. There is no single longitudinal study, so far as we are aware, which details the morbidity and mortality of people at this cultural level. We show here evidence that mortality among adults is quite high compared to contemporary national experience, but are unable to explain this. On the contrary, the impressions gained by countless field workers among primitives have led them to describe their populations as relatively hardy and healthy (e.g., Carr-Saunders, '22; Neel et al., '64). Nutrition seems adequate, and life is generally not inordinately strenuous (except for periods of intensive warfare). The incidence of epidemic infectious diseases is always assumed to have been low among aboriginal tribal populations, and at an early age they show high γ -globulin levels and antibody profiles presumably indicating protection against most of the endemic diseases to which the Indians are exposed (refs. in Neel et al., '68a,b). If future studies can deal with mortality in detail it would be a great service to our understanding of anthropological demography; however, there seem to be few societies left where the introduction of alien diseases has not already taken its toll.

We are still far removed from a comprehensive mathematical model which incorporates all of the demographic characteristics given in this paper, thus setting the stage for attempts at rigorous inferences regarding evolutionary forces. Creating such a model will be the work of the next decade, and hopefully, will be aided by other large-scale biomedical investigations into some of the few remaining quasi-aboriginal populations. It may be properly asked whether a treatment of this complexity is indicated, whether simpler approximations, with regard to genetic processes at least, as summarized by Crow

and Kimura ('68) and Cavalli-Sforza and Bodmer ('71), are adequate. We believe that in many respects they are not, that the more complex models may yield significant differences in a variety of predictions. As noted earlier, a computer simulation treatment of the Yanomama has been developed, as a means of exploring some consequences of population structure which in the absence of a proper model are not yet amenable to formal treatment (Li and Neel, '73). While the model is admittedly imperfect, it is surely adequate for exploratory purposes. The first major problem attacked was the mean survival time in generations (\bar{t}_0) for a mutation which did not alter its possessor's fitness (a "neutral" mutant) and which failed to go to fixation. This survival time is less than half that predicted from the "variance effective population number, N_{ev} " of the simulated populations of four villages, based on formulations of Kimura and Ohta ('69). This is apparently due in large measure to the high infant and childhood mortality as well as to barriers to free gene flow, factors which have much less influence on fluctuations in gene frequency than on mutant survival. Other such empirical studies are projected.

We close this discussion with an appeal to anthropologists working with populations such as the Yanomama to produce comparable bodies of data. We have identified the minimal data necessary in order to construct life tables, the growth rate over the past few decades, the age-specific fertility rates and the ages of each individual in the population. Having these data, one can determine the basic population structure of a group from existing models. We have also identified elements of a complete data set wherein our own material is deficient. These include the rates of abortion and infanticide. We were forced to include some of these elements in an "undetailed infant mortality rate." Similar problems existed with our attempts to detail the variance in fertility patterns among Yanomama adults. Future studies which are able to compile better data in these respects will result in demographic descriptions in which there is less room for uncertainty than that which we were forced to accept. The subject of the origin of human variation is too important for inferences about the population structure

under which it arose to be based strictly on the study of a single tribe. We have not compared our results with those of some other extensive studies on such groups as Australian aborigines or the African bushmen, partly because this study is long already and partly because these other groups seem to have been disrupted significantly more than have the Yanomama. Unfortunately, this important area in the study of human evolution has produced little data whose details could be contrasted with the Yanomama in a very productive way.

LITERATURE CITED

Barclay, G. W. 1958 *Techniques of Population Analysis*. John Wiley and Sons, Inc., New York.

Becher, H. 1960 *Die Surára und Pakidái: Zwei Yanonámi-Stämme in Nordwest brasilien*. De Gruyter & Co., Hamburg, Germany.

Birdsell, J. B. 1953 Some environmental and cultural factors influencing the structuring of Australian aboriginal populations. *Amer. Naturalist*, 87: 171-207.

Brass, W. 1958 The distribution of births in human populations. *Population Studies*, 12: 51-72.

Carr-Saunders, A. M. 1922 *The Population Problem: A Study in Human Evolution*. Clarendon Press, Oxford.

Cavalli-Sforza, L. L., and W. F. Bodmer 1971 *The Genetics of Human Populations*. W. H. Freeman and Co., San Francisco.

Chagnon, N. A. 1968 *Yanomamö: The Fierce People*. Holt, Rinehart and Winston, New York.

——— 1972 Tribal social organization and genetic microdifferentiation. In: *The Structure of Human Populations*. G. A. Harrison and A. J. Boyce, eds. Oxford University Press, Oxford, pp. 252-282.

——— 1974 *Studying the Yanomamö*. Holt, Rinehart and Winston, New York.

Crow, J. F. 1958 Some possibilities for measuring selection intensities in man. *Hum. Biol.*, 30: 1-13.

Crow, J. F., and M. Kimura 1970 *An Introduction to Population Genetics Theory*. Harper and Row Publishers, Inc., New York.

Devereux, G. 1955 *A Study of Abortion in Primitive Societies*. Julian Press, New York.

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

Fisher, R. A. 1930 *The Genetical Theory of Natural Selection*. Dover Publications, Inc., New York (reprinted 1958).

Gershowitz, H., and J. V. Neel Gm and Inv types in seven Indian tribes. Manuscript in preparation.

Gershowitz, H., M. Layrisse, Z. Layrisse, J. V. Neel, N. Chagnon and M. Ayres 1972 The genetic structure of a tribal population, the Yanomama Indians. II. Eleven blood groups and the ABH-Le secretor traits. *Ann. Hum. Genet.*, 35: 261-269.

- Howell, N. 1971 The feasibility of demographic studies in small and remote populations. Paper read at Columbia Ecology Seminar, New York.
- 1974 An empirical perspective on simulation models of human populations. In: *Computer Simulation in Human Population Studies*. B. Dyke and J. MacCluer, eds. Academic Press, New York, pp. 43–57.
- Imaizumi, Y., M. Nei and T. Furusho 1970 Variability and heritability of human fertility. *Ann. Hum. Genet.*, 33: 251–259.
- Keyfitz, N., and W. Flieger 1968 *World Population: An Analysis of Vital Data*. University of Chicago Press, Chicago, Illinois.
- 1971 *Population: Facts and Methods of Demography*. W. H. Freeman and Co., San Francisco, California.
- Kimura, M., and T. Ohta 1969 The average number of generations until extinction of an individual mutant gene in a finite population. *Genetics*, 63: 701–709.
- Kojima, K., and T. M. Kelleher 1962 Survival of mutant genes. *Amer. Naturalist*, 96: 329–346.
- Krzywicki, L. 1934 *Primitive Society and Its Vital Statistics*. The Macmillan Co., London, England.
- Lee, R. B., and I. DeVore (eds.) 1968 *Man the Hunter*. Aldine Publishing Co., Chicago, Illinois.
- Li, F. H. F., and J. V. Neel 1974 A simulation of the fate of a mutant gene of neutral selective value in a primitive population. In: *Computer Simulation in Human Population Studies*. B. Dyke and J. MacCluer, eds. Academic Press, New York, pp. 221–240.
- MacCluer, J. W., J. V. Neel and N. A. Chagnon 1971 Demographic structure of a primitive population: a simulation. *Amer. J. Phys. Anthropol.*, 35: 193–208.
- McArthur, N. 1972 Cross-currents: the statistics of kuru. *Hum. Biol. in Oceania*, 1: 289–298.
- Migliazza, E. 1966 *Cultura materiale degli Scirianá I*. Terra Ameriga, No. 7, Associazione Italiana Studi Americanistici, Geneva, Italy, pp. 3–13.
- 1967 *Cultura materiale degli Scirianá II*. Terra Ameriga, No. 8, Associazione Italiana Studi Americanistici, Genova, Italy, pp. 9–16.
- 1972 *Yanomama Grammar and Intelligibility*. Ph.D. Thesis, University of Indiana, Bloomington.
- Motulsky, A. G., G. R. Fraser and J. Felsenstein 1971 Public health and long-term genetic implications of intrauterine diagnosis and selective abortion. In: *Symposium on Intrauterine Diagnosis*. D. Bergsma and A. Motulsky, eds. Birth Defects Original Article Series, 7(5): 22–32.
- Nag, M. 1962 *Factors Affecting Human Fertility in Non-Industrial Societies: A Cross-Cultural Study*. Yale University Publications in Anthropology, No. 66.
- Neel, J. V. 1970 Lessons from a "primitive" people. *Science*, 170: 815–822.
- 1972 The genetic structure of a tribal population, the Yanomama Indians. I. Introduction. *Ann. Hum. Genet.*, 35: 255–259.
- Neel, J. V., and N. A. Chagnon 1968 The demography of two tribes of primitive, relatively unacculturated American Indians. *Proc. Nat. Acad. Sci.*, 59: 680–689.
- Neel, J. V., and R. H. Post 1963 Transitory "positive" selection for colorblindness. *Eugen. Quart.*, 10: 33–35.
- Neel, J. V., and R. H. Ward 1970 Village and tribal genetic distances among American Indians, and the possible implications for human evolution. *Proc. Nat. Acad. Sci.*, 65: 323–330.
- Neel, J. V., A. H. P. Andrade, G. E. Brown, W. E. Eveland, J. Goobar, W. A. Sodeman, Jr., G. H. Stollerman, E. D. Weinstein and A. H. Wheeler 1968b Further studies of the Xavante Indians. IX. Immunologic status with respect to various diseases and organisms. *Amer. J. Trop. Med. Hyg.*, 17: 486–498.
- Neel, J., T. Arends, C. Brewer, N. Chagnon, H. Gershowitz, M. Layrisse, Z. Layrisse, J. MacCluer, E. Migliazza, W. Oliver, F. Salzano, R. Spielman, R. Ward and L. Weitkamp 1972 Studies on the Yanomama Indians. In: *Human Genetics. Proc., IV Int. Congr. Hum. Genet.*, Paris, Amsterdam: Excerpta Medica, pp. 96–111.
- Neel, J. V., W. M. Mikkelsen, D. L. Rucknagel, E. D. Weinstein, R. A. Goyer and S. H. Abadie 1968a Further studies on the Xavante Indians. VIII. Some observations on blood, urine and stool specimens. *Amer. J. Trop. Med. Hyg.*, 17: 474–485.
- Neel, J. V., F. M. Salzano, P. C. Junqueira, F. Keiter and D. Maybury-Lewis 1964 Studies on the Xavante Indians of the Brazilian Mato Grosso. *Amer. J. Hum. Genet.*, 16: 52–140.
- Ramos, A. R. 1972 *The Social System of the Sanuma of Northern Brazil*. Ph.D. Thesis, University of Wisconsin, Madison.
- Rappaport, R. A. 1967 *Pigs for the Ancestors: Ritual in the Ecology of a New Guinea People*. Yale University Press, New Haven, Connecticut.
- Salzano, F. 1963 Selection intensity in Brazilian Caingang Indians. *Nature*, 199: 514.
- 1972 Genetic aspects of the demography of American Indians and Eskimos. In: *The Structure of Human Populations*. G. A. Harrison and A. J. Boyce, eds. Oxford University Press, Oxford, England, pp. 234–251.
- Salzano, F. M., J. V. Neel and D. Maybury-Lewis 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., and J. V. Neel 1972 The effects of parental consanguinity and inbreeding in Hiro, Japan. V. Summary and interpretation. *Amer. J. Hum. Genet.*, 24: 425–453.
- United Nations 1967 *Demographic Yearbook*. United Nations, New York.
- Vayda, A. P. (ed.) 1969 *Environment and Cultural Behavior: Ecological Studies in Cultural Anthropology*. Natural History Press, New York.
- Wagener, D. K. 1973 An extension of migration matrix analysis to account for differential immigration from the outside world. *Amer. J. Hum. Genet.*, 25: 47–56.
- Ward, R. H., and J. V. Neel 1970 Gene frequencies and microdifferentiation among the Makiritare Indians. IV. A comparison of a genetic network with ethnohistory and migration matrices: a new Index of Genetic Isolation. *Amer. J. Hum. Genet.*, 22: 538–561.
- Weiss, K. M. 1972 A general measure of human population growth regulation. *Amer. J. Phys. Anthropol.*, 37: 337–344.

- 1973a Demographic Models for Anthropology. Society for American Archaeology, Memoirs No. 27.
- 1973b A method for approximating age-specific fertility in the construction of life tables for anthropological populations. *Hum. Biol.*, 45: 195-210.
- Weitkamp, L. R., T. Arends, M. L. Gallango, J. V. Neel, J. Schultz and D. C. Shreffler 1972 The genetic structure of a tribal population, the Yanomama Indians. III. Seven serum protein systems. *Ann. Hum. Genet.*, 35: 271-279.
- Wiener, A. S. 1931 Chances of detecting interchange of infants, with special reference to blood groups. *Z. Indukt. Abstamm. Vererbung.*, 59: 227-235.
- Wynne-Edwards, V. C. 1962 *Animal Dispersion in Relation to Social Behavior*. Hafner Publication Co., Inc., New York.
- Zerries, O. 1964 *Waika: Die Kulturgeschichte Stellung der Waika-Indianer des Oberen Orinico im Rahmen der Volkerkunde Südamerikas*. Band I. Klaus Renner Verlag, Munich, Germany.