Demography and Genetics at the Tribal Level: The Xavante as a Test Case

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The anthropological literature is full of reports on the impact of the meeting of peoples with different cultures, for instance, European colonizers and Amerindians [see, e.g., Verano and Ubelaker 1992] and evolutionary inferences about the type of population structure that prevailed at the tribal level of our history [e.g., Hawkes et al. 1998]. Intensive, quantitative investigations of groups living at this stage of subsistence are, however, relatively few.

The evolutionary fate of a given group basically depends on two parameters, birth and death. The relationship between these events and population size in humans is the concern of demographers, while biologists in general rely on life-history methods in attempts to quantify the factors responsible for these phenomena and interpret them [Stearns 1992]. Two types of problems arise when we try to use this kind of information for Homo sapiens. First, demographic theory is mainly concerned with large populations, but for most of our evolutionary history groups were small. Second, in communities that most closely approach the type of population which existed in the past it is very difficult to obtain reliable data because of taboos with regard to the dead and the lack of written records. Therefore, researchers have to rely on the statements and memory of the individuals interviewed, which may produce incorrect information. The way to circumvent this problem is to cross-check the data extensively by obtaining as many independent sources of information as possible. This, however, is a slow process, and because it demands long periods in the field it is sometimes impossible.

The Xavante of the Brazilian Mato Grosso are unusual in that one of their populations (São Domingos, also called Rio das Mortes or Eténếtêpá) has been followed for nearly half a century. They were first studied in 1957–58 by the anthropologist David Maybury-Lewis, who spent a year with them and collected a detailed pedigree of the group. In 1962 he returned to this community with a group of biomedical investigators. At that time a new demographic survey was conducted, and the information obtained was carefully compared with the earlier data to detect errors or omissions. In addition, a whole battery of genetic tests available at the time was applied to the blood samples that were collected. The revised and updated pedigree, the genetic data, and the anthropological information were published by Neel et al. (1964) and Maybury-Lewis [1967].

Ten years later one of us (Flowers) lived with the group for 14 months, obtaining data for a comparative ecological study of Central Brazilian Indian populations (Gross et al. 1979). A new demographic census was performed, the genealogical information obtained by Maybury-Lewis (1967) verified, and birth and death events recorded. Returns of Flowers to the field in 1988, 1990, 1994, and 1996 as part of new, extended biomedical and genetic investigations (Santos et al. 1997, Salzano et al. 1997) made possible further genealogical verifications, corrections, and updating covering a period of about 85 years (from 1905, the estimated year of the first birth, to 1990). A general review of the demographic results obtained up to that time was published by Flowers (1994).

The present study integrates the demographic and genetic data obtained over these years with life-history theory and compares these results with those obtained for three South American Indian groups, Yanomama, Mekranoti, and Ache, for which there are detailed demographic data [Neel and Weiss 1975, Werner 1983, Hill and Hurtado 1996]. We also compare our findings with information on the !Kung [Howell 1979].

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1. © 2001 by the Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/2001/4201-0008$1.00. This paper is dedicated to James V. Neel, who coordinated the first genetic study of the Xavante in the 1960s and whose paradigmatic personality and dedication to science are a permanent stimulus to all of us. Thanks are due to Marilene D. Bandeira for help in the statistical analyses and to the Fundação Nacional do Índio (FUNAI) for permission to study the Indians and for logistic assistance. The Indian leaders and the subjects of the investigation were adequately informed about the aims of the study and gave their approval, which is also gratefully acknowledged. Financial assistance was provided by the Programa de Apoio a Núcleos de Excelência, the Financiadora de Estudos e Projetos, the Conselho Nacional de Desenvolvimento Científico e Tecnológico, the Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul, the Wenner-Gren Foundation for Anthropological Research, and the MacArthur Foundation.
**Subjects and Methods**

The Xavante are a Ge-speaking tribe. In the early 18th century, when they first entered into contact with neo-Brazilians, they lived in what is now the state of Goiás; in the middle of the 19th century, however, perhaps in an effort to live apart from outsiders, they crossed the Araguaia River and settled in eastern Mato Grosso, remaining isolated there for about 80 years. During the 1940s the Brazilian government, through its indigenist institution, made a special effort to establish friendly contacts with them.

One of the first groups to make peaceful contact was the one we studied (Eteńita). At the time it was ruled by Apowe, a very powerful headman who made history not only because of his political influence but also because of the alleged number of enemies he or his group had killed and the number of offspring he had fathered (Neel et al. 1964). The postcontact history of the Etěnita Xavante followed the usual pattern of stress from epidemic disease and social disruption, but by 1976–77 their living conditions had improved and they were engaged in a struggle to drive outsiders from their land. They were largely successful in this endeavor, and ten years later their reservation was almost 50% larger than in 1977. Their population had doubled, but they preserved a strong sense of identity.

The successive visits made by Maybury-Lewis and two of us (Flowers and Salzano) to the village provided the possibility of extensively cross-checking the information obtained at different points in time. Moreover, all the data were exhaustively examined through the information obtained from different individuals. Since on two occasions [1958 and 1976–77] the fieldwork lasted for a year and 14 months, respectively, we also had the opportunity to become fully acquainted with all village members and to acquire their confidence for the consideration of delicate reproductive matters. In the laboratory all the data were stored and analyzed using computerized methods, with repeated cross-checking. Therefore, although we do not claim that the set is flawless, we feel that it is the best that can be obtained for the period of study.

In a previous analysis of the demographic data [Flowers 1994], three periods of the community life of this group could be discerned: period 1 (before 1957), when interactions with non-Indians were sporadic and the Xavante were still seminomadic; period 2 (1957–71), when they suffered from epidemic diseases and experienced the resulting social disruption; and period 3 (1972–90), when they settled at their present location and population recovery began. Because of the important differences in mortality and fertility patterns observed in these periods, the integrated data obtained by Flowers as described above were subdivided accordingly in some of the analyses presented herein, recognizing that this procedure would produce a reduction in sample sizes. Because the methodology of period analysis involves only years lived within the time span considered, an individual could participate as a young person in one period and as an adult in another. This approach led to truncation of some lifetimes in periods 2 and 3, when years lived in the previous period(s) were excluded from the analyses. This approach followed the main directions given in Hill and Hurtado [1996:100, 183]. Two hundred and sixty-one males and 250 females were considered.

For each period, the age-specific mortality rate \(q_y\), the probability of death for each one-year interval and the estimate of the survival function \(l_x\) were obtained using the method of Kaplan and Meier [1958], while the log-rank test [Mantel 1966] was used to compare different survival curves. The reproductive value \(V_x\), as defined by an equation developed by Fisher [1930; see also Hill and Hurtado 1996:19–20], was calculated for each study period. \(V_x\) measures the expected contribution of an individual to the population gene pool [in units of currently existing offspring] from age \(x\) onward. It weights the contribution of individuals of different ages to population growth and compares the sensitivity of fitness to events at different ages [Stearns 1992:26]. The equation is as follows:

\[
V_x = \sum_{y=0}^{\infty} l_x m_x e^{-\alpha (y-x+1)},
\]

where \(V_x\) is the reproductive value at age \(x\), \(m_x\) is the fertility rate at age \(y\), \(l_x\) and \(l_y\) are the probability of surviving from birth to the beginning of age \(y\) or \(x\), \(\alpha\) represents the age of the oldest individual who reproduced, and \(r\) is the instantaneous growth rate of the population. Parents’ ages at each childbirth were obtained by retrospective estimation of the mother’s [or father’s] age at delivery according to the recorded age of the child. Person-years were then calculated for each parent age, and the age-specific fertility estimates were obtained by dividing the total number of births in each age-interval by the total number of person-years in this interval. Although the data will be presented here in an abridged form, the age-specific fertility rates employed in the above equation were estimated as the averages for five-year intervals to reduce errors due to small sample size. An exception occurred in the first period, for which we lumped together data for women 35–44 years old.

The rate of population increase \(r\) was obtained for each study period, according to the formula

\[
r = \ln[\text{Net Reproduction Rate}]\mu,
\]

where the net reproduction rate is the average number of daughters a woman would have if she were to experience the given mortality and fertility rates and \(\mu\) is the mean age of childbearing [Newell 1988:122].

Fitness \(W_x\), as proposed by Hill and Hurtado [1996:387], essentially measures the average number of gene copies of an individual [herein called “ego”] found in all descendants when the value of each is calibrated to that of a newborn. \(W_x\) was calculated for each man of age 40 or older and woman of age 35 or older, according to


\[ W_i = \sum_{j=1}^{n} V_{ij} s_{ij} \]

where \( W_i \) is the fitness of ego at \( x \) years after ego's birth, \( n \) is the number of direct genetic descendants of ego, \( V_{ij} \) is the reproductive value of the \( i \)-th descendant who is \( y \) years old at \( x \) years after ego's birth, and \( s_{ij} \) is the coefficient of genetic relationship between ego and his/her \( i \)-th descendant (\( g = 0.5 \) for offspring, 0.25 for grandoffspring, and so on).

The fitness values of the Eténitépa Xavante obtained as indicated above were compared among sexes and study periods and among phenotypes of 17 protein genetic systems. The details of the phenotype determinations have been presented elsewhere [Neel et al. 1964, Salzano et al. 1997]. Briefly, the blood and saliva obtained in the field were appropriately stored and submitted to laboratory analysis using immunological or electrophoretic (separation by the electric charges of the molecules) techniques. Lack of genetic information for all individuals evaluated in relation to fitness led to a smaller subsample for this level of analysis. Differences in sample sizes among systems are due to eventual typing problems related to blood conservation and/or to unavailability of reagents.

\( F \) and \( t \) tests [and in one case a Wilcoxon-Mann-Whitney] were performed using the SPSS® program to compare the \( W_i \) values in the different subsamples [SPSS, Inc. 1998].

RESULTS

Figure 1 presents the survivorship functions for Eténitépa Xavante males and females in three distinct periods of community life. Significant \( (p = 0.003 \text{ to } p < 0.001) \) differences occur between periods \( 1 \) and \( 3 \) as compared with period \( 2 \) both for males [log-rank \( \chi^2 \) test, \( d.f. = 1 \), period \( 1 \) versus \( 2, 11.91; 3 \) versus \( 2, 16.04 \)] and females \( (\chi^2, \text{ period } 1 \text{ versus } 2, 8.68; 3 \text{ versus } 2, 15.49) \). No differences were observed between periods \( 1 \) and \( 3 \) (males \( \chi^2 = 1.36, p = 0.244 \); females \( \chi^2 = 0.02, p = 0.898 \)).

Since because of small sample sizes individual values would unduly influence the estimates, we decided to derive life expectancies considering the whole sample instead of dividing it by periods [but the numbers obtained in the separate time-intervals on this and other aspects of our analysis are available on request]. The values were similar for men [44.9 years] and women [45.9]. These are high life expectancies for people living under the environmental and social conditions experienced by the Xavante. The figures observed in the Ache tribe are 37.8 and 37.1, respectively, for persons living in the forest and 50.4 and 45.6 for Indians living on reservations [Hill and Hurtado 1996:196–203]. Quite different expectations are those for the Yanomama, as calculated from the life-table model obtained by Neel and Weiss (1975): 21.5 for males and 19.8 for females. These researchers, however, employed different models of age distribution, mortality, growth rate, and age-specific fertility from those used by Hill and Hurtado [1996] and by us. Though high life expectancies can reflect the underenumeration of infant deaths—a problem that challenges demographic studies in many contexts—there is no reason to think that such underenumeration would be more severe in the data set reported here than in the other cases in which we compare the Xavante.

Age- and sex-specific fertility estimates \( (m_i) \) for the Eténitépa Xavante were derived from the information on the reproduction of 60 males and 80 females and are shown in figure 2. Women start their reproductive lives earlier than men and finish them 20 years earlier, as is usual in our species. The three periods of study presented different fertility patterns. In period \( 1 \) an unexpected saddle curve was observed, due mainly to the high fertility of two women who together had six children when they were 30–34 years old. In period \( 2 \) the fertility rates were generally lower than in the other periods. At the peak of the Eténitépa female fertility rate, in the period with the more reliable data (period \( 3 \), mothers 20–24 years old), the average woman delivered a child every 2.5 years. Men, in contrast, had a general 0.3 fertility plateau at the 25–44-year age-class, decreasing to almost 0 at 55–59.

The exception was period \( 1 \), with higher rates in the 40–50-year age-class. This proved to be the fertility profile of one individual [Apowe] who because of his high rank in the group had better chances to reproduce. These data were compared with those obtained among the Yanomama [Neel and Weiss 1975], Mekranoti [Werner 1983], Ache [Hill and Hurtado 1996], and !Kung [Howell 1979]. Despite the decline of values during the contact period, the Xavante women consistently showed higher fertility estimates in the 15–24-year interval. A similar pattern is presented by the Yanomama, the Mekranoti in contact times, and the !Kung [these, however, with much lower rates]. The Ache women presented their peak of fertility in the 25–39-year age-interval in both forest and reservation times.

The rates of population increase \( r \) were 0.0410 for period \( 1, 0.0066 \) for period \( 2 \), and 0.0408 for period \( 3 \), as expected considering the demographic characteristics described above.

The age- and sex-specific survivorship and fertility data were used to estimate the reproductive value distribution of the Eténitépa Xavante, and the results are shown in figure 3. Males presented a maximum of 3.3–7.4 expected children depending on the study period at about age 22, while the maximum for females was 4.5 at age 15. Males showed more variation between periods, and their reproductive life span was longer. \( V_i \) greater than \( 1 \) [the expected value in newborns] occurred until the age of 34 in females and 45 in males. The Ache [Hill and Hurtado 1996:415] showed similar ranges, but in the forest period values greater than \( 1 \) occurred up to age of 37 in females and 43 in males, while in reservation times both males and females showed these values until about age 35 only. That is, while the comparison for women shows equivalent results, the Xavante males’ reproductive span is at least ten years longer than that of the Ache males.

Fitness values \( \{W_i\} \), representing the individual’s con-
Fig. 1. Survival \( l_x \) by sex and age in three periods \((P_1, P_2, P_3)\) of a Xavante community. Sample sizes for males: period 1, 42; period 2, 103; period 3, 222; for females, period 1, 50; period 2, 98; period 3, 212.

Distribution to subsequent generations, were obtained for each individual in the final years of his/her reproductive life. This criterion produced a sample of 30 Xavante males 40 or more years old and 28 females aged 35 or older. Table 1 summarizes the results obtained for individuals whose reproductive cutoff occurred in one of the three different study periods. \( W_x \) varied from 3.9 to 17.2 (average 9) in males and from 1.0 to 17.7 (average 11) in females. The difference is not statistically significant, despite some tendency favoring higher values in women \((p = 0.088)\). The apparent greater range observed in women is due to only one individual from period 1 with \( W_x = 1.0\); all the other values in this period varied between 5.2 and 17.7. A comparison between periods showed a clear “no-difference” pattern \((p > 0.60)\).

Comparing our data with the \( W_x \) values obtained by Hill and Hurtado (1996:388–416) in the Ache, we found that the most successful Ache male would produce 22 genetic equivalents of himself, whereas his counterpart...
Xavante male would produce 17. For females the values are more similar—Ache 17, Xavante 17.7.

The absence of significant differences among periods and between sexes prompted us to pool the data in a single sample for the following analyses.

Our data produced no evidence for a long-term fitness cost due to high fertility. The relationship between \( W_x \) and the total number of descendants [ND] is linear \( W_x = 1.58 + 1.24 \text{ ND}; n = 58; \text{ product-moment correlation coefficient } 0.924; p < 0.001 \). Considering now the relationship of \( W_x \) to the number of children [NC], the equation is \( W_x = 1.74 + 1.36 \text{ NC}; n = 58; \text{ correlation coefficient } 0.890; p < 0.001 \). These results suggest that for the Etenitépa Xavante the total number of descendants is a good measure of the long-term (at least in the periods considered) genetic contribution of one individual to the next generation [Hill and Hurtado 1996:388].

We used \( W_x \) to compare the phenotypes observed in 17
protein systems in relation to their fitness (table 2). The objective was to verify whether specific genetic regions would influence the amount of biological influence a person would have on subsequent generations. No significant difference was found between phenotypes, the smallest p value (0.057) probably being due to a reduced sample size for the ACP system.

**Discussion and Conclusions**

No claims are being made that we are dealing with a pristine tribal society followed since its first contacts with the outside world. Although the Xavante, prior to 1940, lived in remote areas, they may have received indirect influences on their health, technology, and crops from the non-Indians present in their general region. In addition, the demographic changes which occurred in period 3 were undoubtedly influenced by the provision of basic medical care, such as immunization for various infectious diseases, and better nutrition, made possible by several aid agencies. But the fact remains that our data provide the best approximation that can be obtained

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**Fig. 3.** Reproductive values \(V_x\) by sex and age in three periods \(P_1, P_2, P_3\) of a Xavante community.
in cases like this one of transition from a tribal to a nontribal pattern of life.

The main findings of our study can be summarized as follows: (a) There are no significant differences in life expectancies among Xavante males and females. The high values obtained in the total sample [45 years for males, 46 years for females] reflect the highly successful demographic history of the group, which doubled its population between 1977 and 1990. (b) Xavante women present higher fertility rates at younger ages compared with those obtained in other South American Indian tribal groups. (c) The reproductive value distributions show longer life spans for males than for females and for Xavante males as opposed to Ache males. (d) The average value and the variability in fitness of Xavante males are similar to those of females, an unexpected result in a polygynous society such as this one. The results probably reflect the fact that, obviously, both males and females are needed for reproduction; in addition, however, generally all females are engaged in the reproductive process [all women marry at an early age, and after the death of a polygamous male they immediately remarry a generally younger male]. (e) In about the same period of time, Xavante male and female fitness values are similar to those presented by the Ache. (f) The various phenotypes for blood-group and other protein genetic systems do not differ in relation to estimated adaptive values.

Attempts to apply life-history approaches to hunter-gatherer or simple-agriculture human communities are few. An excellent review of such studies is provided by Kaplan (1996). Studies of the evolutionary implications of fertility and mortality differences among the Kalahari (Kung [Pennington and Harpending 1988, Harpending, Draper, and Pennington 1990]) and predictors of fecundability and conception intervals among the Dogon (Strassmann and Warner 1998) are good examples. More studies about intergeneration correlations in fertility and mortality are clearly needed, since in small-scale societies status and clan affiliation may greatly influence the fate of a person’s genes. Especially here, the integrated efforts of cultural anthropologists, demographers, and geneticists are needed to obtain reasonably accurate eval-

| Locus       | Phenotypes Compared | N   | F or t Test | p     |
|-------------|---------------------|-----|-------------|-------|
| MN          | M, MN, N            | 39  | F = 0.604   | 0.552 |
| Ss          | S, Ss, s            | 38  | F = 0.409   | 0.667 |
| P           | P[+1, P[+1] | 39  | t = 0.495   | 0.624 |
| Rh-Cc       | C, Cc, c            | 39  | F = 0.682   | 0.384 |
| Rh-Ee       | E, Ee, e            | 39  | F = 0.183   | 0.834 |
| Duffy       | a[+1, a[+1] | 39  | t = 0.810   | 0.423 |
| Diego       | a[+1, a[+1] | 38  | t = 0.717   | 0.478 |
| Kidd        | a, ab, b            | 30  | F = 2.269   | 0.123 |
| ABH Secretor| Sec, non-sec       | 26  | t = 0.383   | 0.705 |
| ACP         | A, AB, B            | 9   | F = 4.789   | 0.057 |
| ESD         | 1, 12, 2            | 8   | F = 3.382   | 0.118 |
| GLO         | 12, 2               | 9   | –           | 1.000 |
| PGM 1       | 1, 21               | 9   | t = 1.323   | 0.227 |
| HP          | 1, 12, 2            | 33  | F = 0.474   | 0.627 |
| HP          | 0, 1, 12, 2         | 39  | F = 0.336   | 0.700 |
| TF          | C1, C1C2            | 8   | t = 0.370   | 0.734 |
| GC          | 1, 12, 2            | 38  | F = 2.694   | 0.052 |
| Gm          | a, ax               | 29  | t = 0.383   | 0.704 |

*Data from 18 males age 40 or older and 22 females age 35 or older.

†Obtained from a Wilcoxon-Mann-Whitney test.

**Table 2**
Comparison of Fitness \( W^f \) Values Among Phenotypes, Considering 17 Genetic Loci

| Table 1 | Fitness \( W^R \) of Eténtépa Xavante Males and Females in Three Different Periods of Their History |
|---------|--------------------------------------------------------------------------------------------------|
| Period  | Males                                                                                             | Females                                                                                     | Total                                                                                     | t Test Between Sexes | p     |
|---------|--------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------|----------------------|-------|
|         | Mean ± SD N                                                                                       | Mean ± SD N                                                                                  | Mean ± SD N                                                                                  | Between Sexes        |       |
| Before 1957 | 7.9 ± 4.1                                              | 11.0 ± 4.7                                                                                   | 8.7 ± 4.1                                                                                   | –                    | –     |
| 1957–71 | 8.4 ± 3.5                                              | 10.9 ± 3.5                                                                                   | 9.3 ± 3.6                                                                                   | –                    | –     |
| 1972–90 | 9.6 ± 4.1                                              | 10.6 ± 4.3                                                                                   | 10.2 ± 4.2                                                                                   | –                    | –     |
| All periods | 8.9 ± 3.8†                                              | 10.7 ± 4.0‡                                                                                   | 9.8 ± 4.0‡                                                                                   | 1.74                 | 0.088 |

*Note: ANOVA among periods: males, \( F = 0.0, p = 0.980 \); females, \( F = 0.49, p = 0.616 \); total, \( F = 0.48, p = 0.622 \).

†Range 3.9–17.2.

‡Range 1.0–17.7; most values between 5.2 and 17.7, a single value equal to 1.00.
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