IV. GENETIC COMPOSITION OF SOUTH SINAI BEDOUIN TRIBES

Effective Size Of The Population

Three major components are here considered when determining size of biological populations, , namely:

(1) Total number of individuals existing in a group at a given point of time;

(2) Breeding size, i.e., total number of individuals of the group in their potential reproductive period (15-45 years of age for female); and

(3) Effective size, meaning the total number of individuals in the population who mate and produce progeny.

The overall size of a particular population group is usually determined by a population census. From the standpoint of genetic drift, the overall population size is not relevant, but in terms of age and sex data available, it does enable one to compute what part of the population will directly transmit its genes to the next generation. If the overall size of the Muzeina tribe is 3056 individuals, and by Ben-David's (1978) age pyramid 39.6% of the population fall within the 15-45 years age group, which is the reproductive group in the tribe, then the size of the breeding group will be somewhat greater than 1200 individuals. Even if we assume that Ben-David`s age pyramid is not precise, we can still estimate the number of individuals in the breeding group by arbitrarily taking a third of the population. We should add that in "simple" societies the three reference groups, namely, the pre-reproductive, the reproductive and the post-reproductive (classification according to Bodenheimer, 1958), are unequal in size, with the reproductive group usually somewhat larger than the other two (Bodmer and Cavalli-Sforza, 1976, p.394). In an "ideal" population, the reproductive group is comprised of an identical number of males and females, size is constant throughout time, there is random mating, each male adult has only a single wife, and each individual of the parent generation produces an equal number of offspring. Only in such an "ideal" population are the size of the breeding group and the effective size of the population identical. In this case, the variance of the random deviation of gene frequencies is $q(1-q)/2N$, and the rate of decay is $1/2N$ (Li, 1968, p.320). In most human populations, including the Bedouin, such an ideal situation does not exist and therefore one needs to compute the effective size of the population.

In large populations, random variations in number of children produced by individuals with different genotypes have no significant effect on gene frequency; but in small populations such variations can have great significance with respect to gene frequency (Li, 1968).

Factors influencing effective size

The present chapter will deal with the wide gamut of factors which exert an influence on the effective size of the Bedouin population. Such factors include a) differential fertility, b) sex ratio, c) polygamy, d) temporary changes in population size, and e) inbreeding.

a. Differential fertility.

In the Bedouin groups, the `differential fertility' variable is a decisive factor in determining the size of Ne and has two different aspects, namely, 1) the differential fertility within a given Xi generation among Xnij generations, and 2) the differential fertility between generations Xni and Xnj which is the mean fertility of the population that changes from generation to generation. For the last two generations (G14&G15), one needs to take a high mean estimate of 4.0 children per family surviving to adulthood (it is not identical with the mean number of living children per family!), whereas for previous generations (G1-G13), based on the data of Ben-David (1978), the estimate would be 2.9 children per family.

b. The sex ratio

The efect of the sex ratio on the effective size (N_e) of a population comprising N_m+N_f inbred individuals can be calculated as follows:

1. $N_e=4N_mN_f/(N_m+N_f)$

Numerical inequality of the two sexes will thus invariably diminish the larger `breeding size' to a smaller `effective size'.

The ratio of males to females in the Bedouin population is the subject of controversy in the literature. According to Ben-David (1978, p.111), the mean sex ratio for the overall South Sinai Bedouin population (averaged for all ages) was 118; according to Nir (1987) it was 109. The ratio which we obtained from the Hams records is 128.1 for G15 and 106.9 for G16. In the age group of 15-44 the sex ratio according to Ben-David's data was calculated to be 108. As we have previously shown, sex ratio varied among generations, and under certain circumstances can reach high values. We here decided to use the lowest sex ratio values calculated by us as the representative sex ratio value in the `fertile age' group (15-44 years).

This of course minimized the effect of sex ratio on the effective size of the population, but put us on the safer side. This value will be the basis for all subsequent calculations of demographic parameters.

(N_m=number of males; N_f=number of females.), Kimura and Ohta, 1971, p.34

c. Polygamy

To our knowledge, there are no precise methods for assessing the effect of polygamy on N_e. Most investigators (e.g. Li, 1968; Kimura and Ohta, 1971) make do with the regular formula (No. 1) for computing the influence of the sex ratio on the effective size of the population.

A formula for calculating the effect of polygamy on N_e was proposed by Wright (1931). However, his formula fits only a situation where a husband has three wives. In the Bedouin population, it will be recalled, only a relatively small number of married males (about 1%) have three or more wives. Indeed in most of the polygamous families of the last generation, polygamous males have two wives (Levi, 1979; Nir, 1987). We concluded that perhaps the best way to introduce the effect of polygamy into computation of the Ne without overlooking men married to two women, is to adapt the differential fertility formula devised by Crow and Kimura (1970, p.351), and originally proposed by Wright (1931), which we did as follows:

(2) $N_e = (N\bar{K}-2)/(\bar{K}-1+V_k/\bar{K})$

where $\bar{K}$ = mean number of offspring per family, V_k the variance, and N the number of parents.

By this formula we can compute the N_e for two different N's, namely, N_f = the number of fathers and Nm=the number of mothers:

(3) $N_{ef} = (N_f\bar{k}_t -2)/(\bar{K}\ t-1+vtt/\bar{k}t)$

(4) $N_{em} = (N_m\bar{k}_w -2)/(\bar{k}w-1+vtw/\bar{k}w)$

where kt = mean number of children per father (formula 3), kw = mean number of children per mother (in polygamous families there will be a large disparity between

these two values), vtt = the variance in number of children per father (formula 3) and vtw = the variance in number of children per mother. After computing the N_{em} and N_{ef}, we introduced their numerical values into formula 1 so as to obtain the N_e of the tribe, including the effect of polygamy and sex ratio.

d. Changes in size of Ne in the early generations

In the course of the 16 generations through which the Muzeina tribe has existed as a defined and recognized social group, its effective size underwent frequent change. Regrettably little available information is extant on these changes, and therefore we have assumed a fixed average change per generation. The formula used to calculate the N_e of a tribe after t generations and with population sizes of N_1, N_2...N_t, according to Li, 1968, p.323, would be:

(5) $1/N_e = 1/t \times (1/Ne_1 + 1/Ne_2 + \ldots + 1/Ne_t)$

Thus, effective size of the group at any period in time will be the harmonic mean of the population effective sizes of different generations within the cycle.

To be sure, for a small number of generations and for significant size changes, the mean effective size does not reflect biological reality (see Li, 1968, p.323). However, since we here "used" population sizes in 15 generations, the distortion introduced into the calculation of the mean effective size for the Muzeina tribe might be smaller. In the absence of precise paleodemographic information on the size of the Muzeina tribe in previous generations, the Ne values for the preceding generation were obtained by the following procedure.

We first estimated the net reproductive rate (NRR), which is a measure of the ability of the population to renew itself (Hassan, 1981). The NRR can be here estimated either directly through Hams (blood feud group) records, or by various demographic variables. According to Ben-David's (1978) data, the average number of children surviving to adulthood in the preceding generations (G_1-G_{13}) was 2.9. Assuming a sex ratio of 107.8 for age group 15-44 years, the NRR should approximate 1.39. With the sex ratio around 108, the average number of women surviving to the age of child bearing was probably around 1.39. Hence, the rate of natural increase of population per generation, or Lotka rate (P), for the Muzeina tribe, assuming existing fertility rates continue, will be:

$P = (y \sqrt{R_0}) - 1 = 11.24$ (Hassan, 1981, p.139)

where y is the mean age at child-bearing age (19.6 years) and $R_0 = 0.39$ the excess of females beyond replacement. In such cases the population can grow at a rate of about 11.24 individuals per 1000 females per year.

The rate of population growth (r) is obtained from the equation: $r = \mathrm{Ln}(N_2/N_1)/t$, where N_2 is the population size reached from an initial population N_1 after a particular time period (t). This equation can be simplified to: $r = \mathrm{Ln}R_0/t$. Given a generation span of 20 years (average age of marriages of male and female), the Muzeina tribe, with a NRR of 1.39, would increase at a rate of about 1.48% per year, or approximately 15 persons per 1000.

The relationship between population growth rate and doubling time (Dt) is expressed by the equation: $Dt = 0.6931/r$ (Hassan, 1981). For a growth rate of 1.48% per year, the doubling time would be 46.8 years.

According to the genealogical tree of the Muzeina tribe, it has been in existence about 16 generations as a recognized social unit, or some 320 years. The Muzeina could have doubled its size approximately 7 times at most during this period, given a generation span of 20 years. Knowing the annual rate of increase, the doubling time, the length of time the tribe has existed, and its size at present, we can calculate the size (N) of the tribe in previous generations (e.g., N_{16}=3000; N_{11}=750; N_6=187; N_1=46), and from that number - the effective size (Ne) at each generation.

It should be emphasized that intrapopulation growth from generation to generation is requisite for continuity of the effect of social and biological factors which mold the population into a certain genetic equilibrium. When this does not prevail, e.g. when there is a sharp decrease in population size as a result of an epidemic, the cumulative nature of the sample variance becomes disrupted, which can lead to changes in gene frequency to the point of abrogation of the previous effect. Once the population recovers, however, and starts growing anew, then the same factors will guide it to a new point of genetic equilibrium. The mean N_e which we computed for the last 15 generations is 56.8, which we assume is about the value of the Ne in the eighth generation of the tribe since its inception.

e. Intragroup marriages or inbreeding level

The nature of the mating patterns within a group is a further factor influencing Ne. In a population which encourages consanguineous marriages (e.g. first-cousins), such as the bedouin tribes of the South Sinai, the Ne will be smaller than that in a randomly breeding population of the same size. The reason for this size difference is that the probability for each man in the tribe to marry any one of the women of the tribe who are eligible for marriage is not equal, depending largely on the sizes of the different social structures.

Methods of computing the Ne of previous generations in a population are presented in Appendix 1.

Summary

In the present chapter we assessed the influences of various factors on the effective size of a population, more specifically, on the Bedouin Muzeina tribe. From a genetic viewpoint, we dealt with those factors which lead to disparity in gene frequencies in the group from one generation to the other owing to random deviation stemming from sampling errors. Such deviations are noticeable in small populations such as the Bedouin and can result in random fixation of the loci.

The rate of diminution in the genetic variability of small groups, which could also be called `the rate of loss of heterozygosity' or `the rate of fixation of the loci' (Li, 1968; p.323), is 1/2Ne per generation, where Ne is the effective size of the population. As a result of the aforementioned process, namely, the decline in genetic variability, the more time involved, the more would small isolated populations of equal gene frequency pull apart and diverge from one another, so that after a number of generations, they would become quite different in their genetic makeup even if environmental conditions remained identical (Li, 1968, p.324).

This type of differentiation between groups stems from random variation and from gene fixation also of a random nature and therefore neither has any adaptive significance.

However, the effective size (Ne) of the Muzeina tribe in the sixteen generation (846 members) is still large enough to comprise by itself a central factor in reducing the genetic variability of the tribe. In the next chapter we shall discuss another important mechanism (albeit fortuitous) which affects genetic variability in the Bedouin society.

Marital Patterns And Immigration Rate: Their Effect On The Coefficient Of Inbreeding (F)

By `immigration' we here mean the entry into the tribe in every generation of "foreign" women who in time produce offspring. The phenomenon of male migration is very rare and thus not considered in our forthcoming calculations. Women who emigrate out of the tribe or who enter it without producing progeny are excluded from this category.

Random breeding in small groups of N individuals results in a loss of heterozygotes at a rate of approximately 1/2Ne per generation, if we ignore the factors of immigration and selection. On the assumption of random union of gametes, the less the heterozygosity the larger the value of F per generation. All formulas cited are from Li (1968, p.305), except as noted otherwise. The increment in F is on the order of:

(6) $F_i = 1/2Ne + [(2Ne-1)/2Ne] \times F_{i-1}$

Immigration rate (M), on the other hand, will prevent the group from attaining homozygosity and will shift the gene frequencies of the group towards the mean value for the total population. In such a process the expression S^2_q will diminish in the next generation to $(1-M)^2 S^2_q$ which will lead to a decrease in the value of F by the same proportion, owing to the ratio $F = S^2_q/\overline{q}(1-\overline{q})$.

In this new equilibrium, the value of F_{im} will now decrease owing to the intrusion of immigrants.

(7) $F_{im} = (1-M)^2 \times F_i$ (Wright, 1951)

In fact, formula (7) describes the basic relationships between the F and M values without the effect of selection.

Marital patterns constitute an important indicator as to how the genes are aggregated in the human genotype. Marital patterns are quite variegated in the various world populations. The reasons for such variability are apparently associated with biological, demographic, social, cultural and other factors.

As noted in the chapter on ethnography, in Bedouin society we recognize a number of marital "types" which, apart from their socio-economic implications, also have a fairly defined biological significance. It may be recalled that the marital "types" recognized thus far were based on the Hams (blood feud group), extended family, clan, sub-tribe, and tribal marriages. The main criterion used to define these marital "types" was the common biological background or depth of the two mates, i.e. the number of generations back to a common ancestor of the mates (Fig. 9). The manner in which we translate these marital "types" in biological terms is illustrated in three "schemes", first, the scheme of Hams of Haj Abdulla (Fig. 10); second, the private case of the Hamid Aiyed family (Fig. 11); and third, the "scheme" given in the first chapter (see Fig. 3).

We may consider immigration in Bedouin society on two different social levels, namely:

a. Women taken for marriage from outside Towara tribal suprastructure, and/or from outside her husband's tribe, but from one of the other Towara tribes;
b. Women taken for marriage from her husband's tribe.

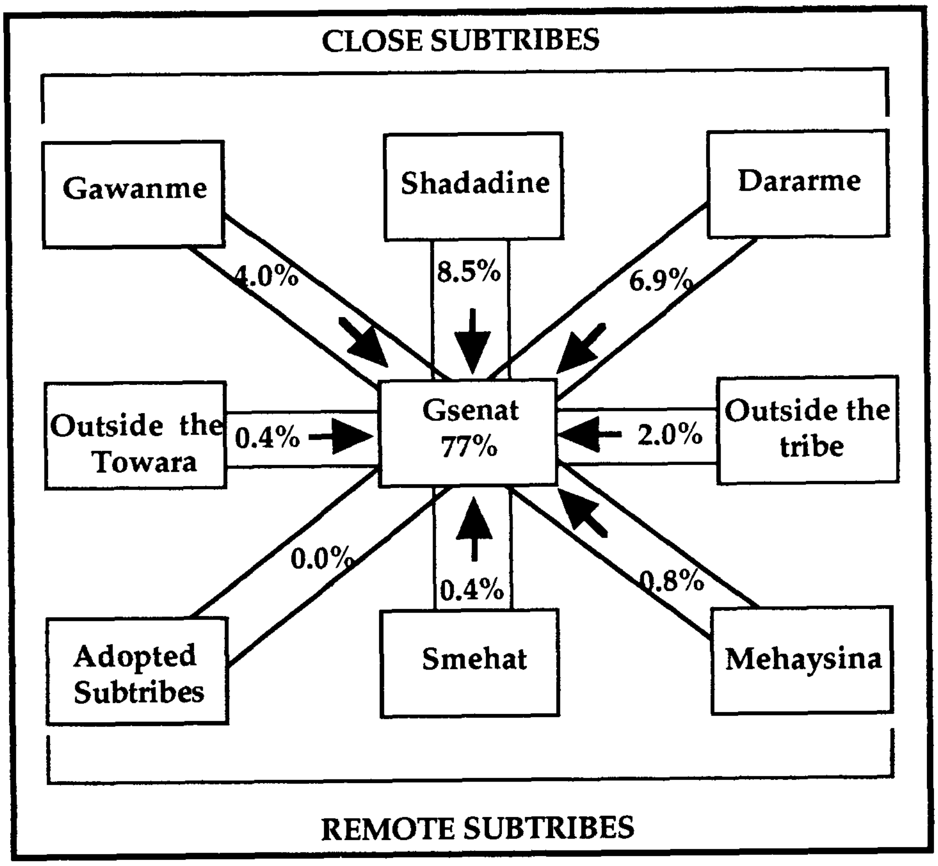
We emphasize again that the data presented herein pertain mainly to computations made for the current generation of the Muzeina tribe only; they do not necessarily reflect the situation prevailing in earlier generations.

a. Marriages outside the tribe.

Despite the numerous testimonies as to the entry of foreign families into the South Sinai Bedouin tribes (see chapter on Tribal Composition), there is little concrete evidence to this effect at present and even in the two preceding generations. The fact that the region of South Sinai is sealed by topographic barriers apparently has precluded regular traffic or communication with neighboring peoples. Thus only 0.4-2.0% of the marriages in the tribe were with women from outside the tribe (Fig. 8). Immigration from outside the Towara into the South Sinai bedouin tribes is extremely small (usually less than 0.5%).

Some tribes do display a stronger tendency to take a wife from outside their Towara tribal suprastructure (e.g. the Gararsha) than others (e.g. the Muzeina). Even within the tribe there are parts (e.g. the sub-tribes) which display different tendencies in this regard. The geographic location of a sub-tribe apparently plays an important role in this respect (Fig. 5). As mentioned, the Gsenat and the Dararme sub-tribes of the Muzeina tribe display such disparity. Thus the former, which lives in the center of the tribal territory, and has neighboring sub-tribes to the east, north and south, hardly accepts brides from outside the Towara, whereas the Dararme sub-tribe, which occupies the periphery of the tribal territory shows greater tendency for such marriages.

FIGURE 8 Women Exchange in Marriage Between the Gsenat Sub-tribe and Other Sub-tribes of the Muzeina Tribe in South Sinai*.



*The rate of "foreign" women entering the sub-tribe Gsenat is 23%; 77% are marriages with women from the same sub-tribe.

Nir (1987) presents somewhat different data in this matter, although he also emphasizes the significant trend for inter-tribal marriages. Nir claims that the rates of such marriages vary among the tribes: the Gebeliya tribe, for example, as a result of its origin and links with the Santa Katharina monastery, is regarded as a `foreign' tribe, and hardly absorbs women from other tribes of the Towara. According to Nir (1987) the Gebeliya is the tribe with the highest frequency of first cousin marriages and the least with outside tribe marriages (<1%). In contrast, the Awlad Said tribe accepts women from practically all the tribes of the Towara and at rates greatly exceeding those of the Gebeliya and Muzeina tribes combined. In the Muzeina tribe, according to our data, the rate of female inflow averages about 3% for each of the last three generations. Nevertheless there are differences also at the sub-tribe level.

b. Marriages within the tribe.

Undoubtedly genealogical ties between the sub-tribes exert a direct influence on the rate of female exchange between them, as illustrated in Fig. 8. First, we note that a large proportion of the females taken as wives comes from within the sub-tribe. For the Muzeina tribe the relevant percentage is approximately 77% (average for all sub-tribes) (G15, table 9). Of the remaining 23% of the marriages, only about 2.4% derive from other tribes or from outside the tribal suprastructure, the Towara, the remainder (20.5%) coming from neighboring sub-tribes. In the Gsenat sub-tribe, for instance (Fig. 8), 19.3% derive from related sub-tribes and only 1.2% from remote sub-tribes. These data suggest that at least in some cases the sub-tribe is the social unit, or alternately, a group of sub-tribes deriving from a common ancestor is such, as for example the Gsenat, Dararme, Shadadine and the Gawanme sub-tribes, all tracing back to an ancestor called `Farag'. Our next step is to try to reconstruct the geneological depth characterizing each type of marriage.

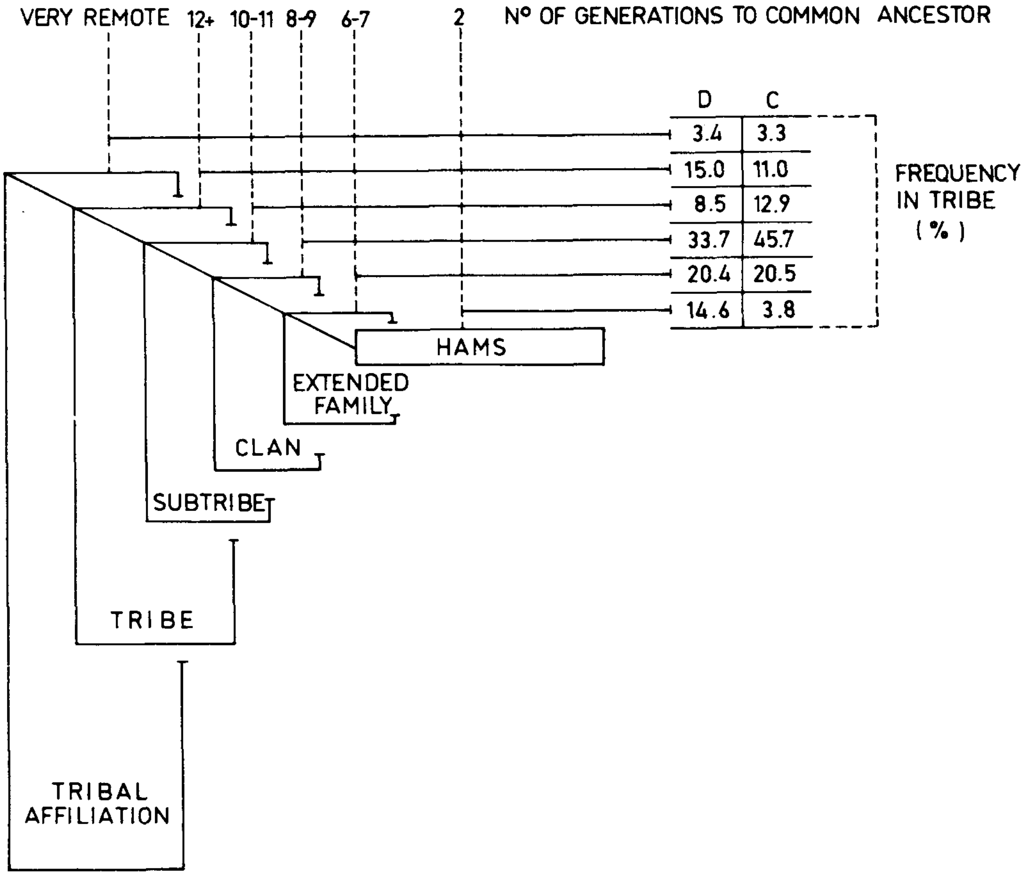
b.1. Hams (Blood Feud Group) Marriages

As noted in the preceding, these marriages are limited to marriages between cousins. Figure 11 describes several such possibilities, e.g. between individuals 1 and 2 who are first cousins, between individuals 1 and 3 who are second cousins, and between individuals 1 and 4 who are third cousins. Marriages between cousins are in most cases marriages with offspring of the father's brother, although there is evidence of other combinations as noted previously. A case in point of first cousin marriages is the one between Muhammed Abdalla Hamid (No. 34) and Mahmuda Saliman Hamed (No. 16) (Fig. 10). In such marriages, both partners need to be represented in the Hams records. *The genealogical depth ranges between two generations for marriages between first cousins to four generations for marriages between third cousins* (Fig. 11). Note that the most remote ancestor is Awad (Fig. 10).

b.2. Marriages in the Extended Family

Here we are dealing with marriages between two individuals of the same family, e.g. between individuals 1 and 5 in Fig. 11. Thus in the marriage between Awad Abdalla Hamed (No. 27) and Hamda Aid Gabali (No. 28) (Fig. 10), the bride comes from a Hams which genealogically belongs to the same family to which the groom's blood feud group belongs (the Breykat). *The common genealogical* *depth for the married couple reaches down to 7 generations.* The remotest ancestor is Breykat (Fig. 11).

FIGURE 9: Number of Generations of the Mates from a Common Ancestor in Various Types of Marriages

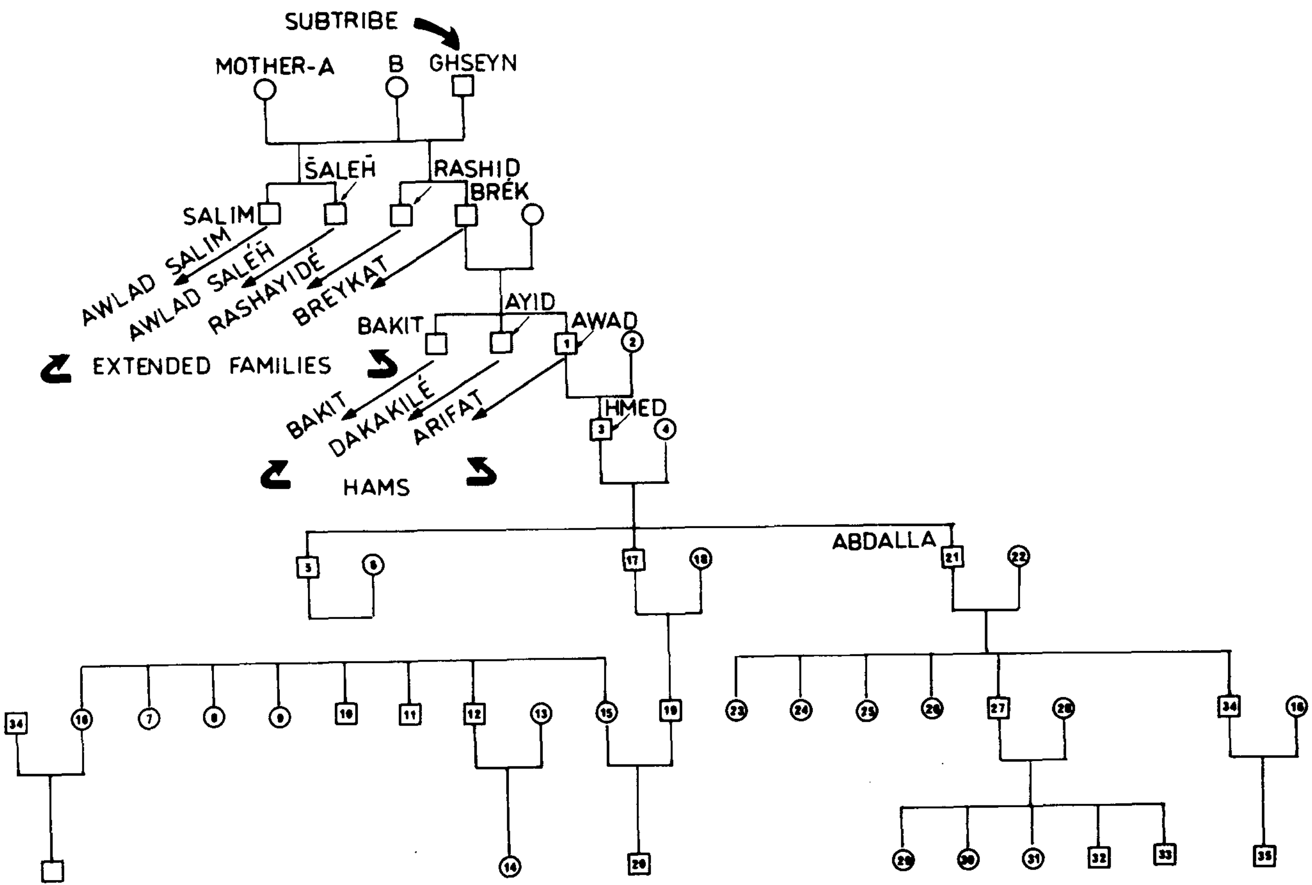


*Marriages outside tribal affiliation not included.

b.3. Clan Marriages

Clan marriages are between individuals belonging to two different families related by a close genealogical tie, for example, a marriage between individuals belonging to families sharing a common ancestor. Thus for the common ancestor Ghse'yn we have the following families: Rashayide, Breykat, Awlad Saleh, Awlad Salim and Hagahige (Fig. 3). Another example is marriage between individuals belonging to families originating from the common ancestor Sari; such families are the Suhub, Bakayte', Abu Sabha and Afe'tiyin (Fig. 3). As observed in Fig. 11, we are dealing with a marriage between individuals 1 and 6. To use a real case which appears in Fig. 10, we take the marriage of Hamid Suleiman Hamid (No. 12) (El-Atrash) to a woman (name not given) who derives from the Rashayide' family (No. 13). *The common genealogical depth for this couple is 9 generations* and their most ancient ancestor is Ghse'yn (Fig. 10).

FIGURE 10: The Origin of the Hams of Haj Abdallah Khamid Awad and its Place within the Genealogical Tree of the Muzeina Tribe

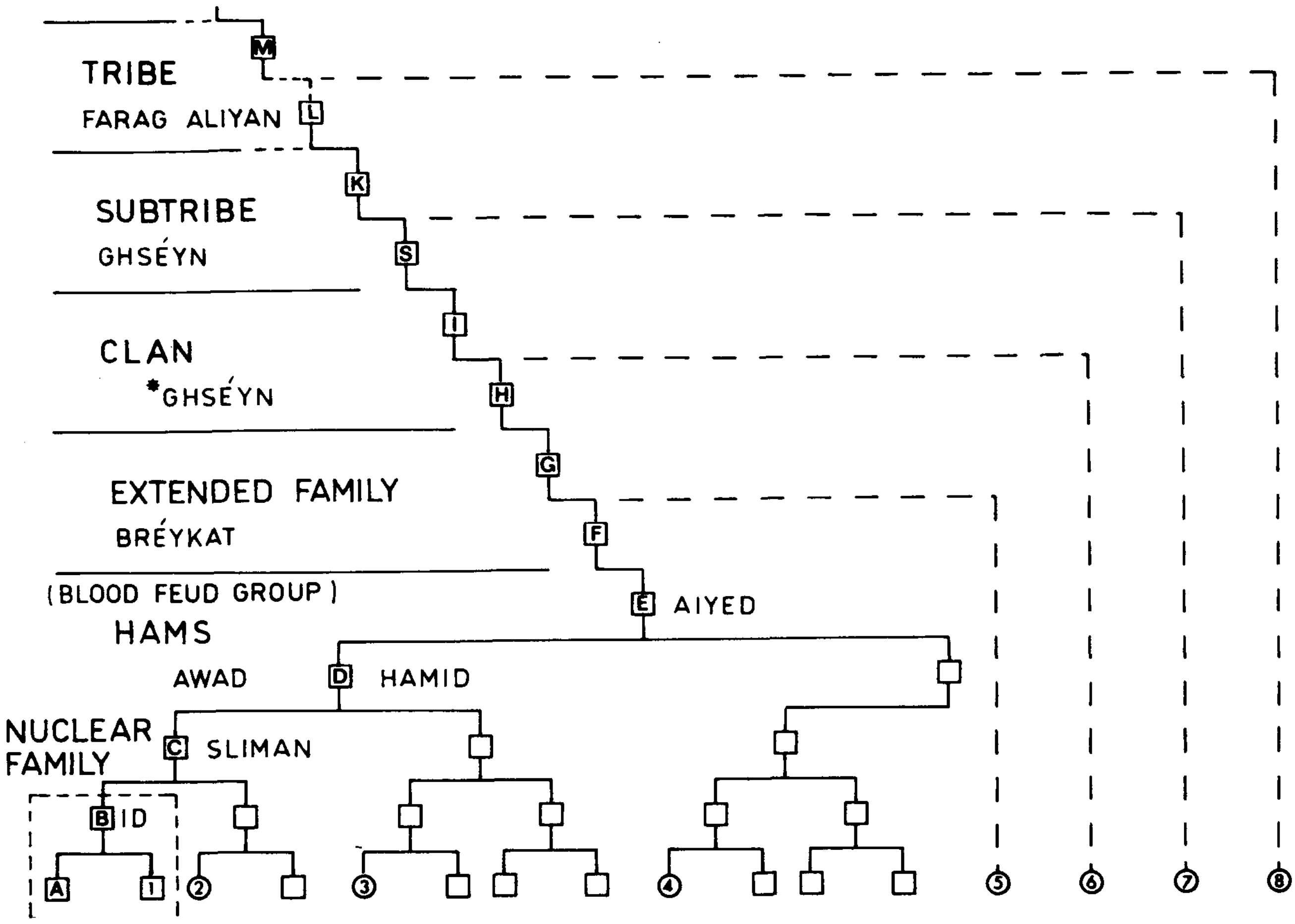


HAMS OF HAJ ABDALLA HAMID AWAD : GSÉNAT, BREYKAT, ARIFAT

Mates discussed in text

34 = Muhammed Abdalla Hamid
16 = Mahmuda Saliman Hamed
27 = Awad Abdalla Hamed
28 = Hamda Aid Gabali
12 = Hamid Sulliman Hamid
13 = a woman derived from the Rashaide
21 = Abdalla Hamid Awad
22 = Gabaliya Saliman A'oula

FIGURE 11: The Genealogical Depth of the Various Marriage Types in the Hamid Aiyed Family.



* One of Ghse'yn's grandsons whose descendants form part of the Gsenat sub-tribe (see Fig. 3).

A - M = Ancestors and their place within the social framework of the Muzeina tribe

1 = Ego

2- 8 = Potential wives for marriages and their genealogical relation to Ego

b.4. Marriages in the Sub-tribe

We here consider marriages between individuals of families that belong to the same tribe, and are genealogically linked through one of the two sons of the tribal founder, either Farag or Alwan (Fig. 3). Such, for example, is the marriage between individual 1 and 8 in Fig. 11, or the marriage between Abdalla Hamid Awad (No. 21) of the Breykat family and Gabaliya Saliman A'ouda (No. 22) of the Shadadine sub-tribe and the Twayirin family (Fig. 10). *The genealogical depth common to these two marrying individuals ranges between 10 and 12 generations* (Fig. 11).

In sum, as noted in the preceding, a precise schema which describes the structuring and development of the tribe from its inception to the present enables one to trace the common "biological" background of each marrying couple. The only information needed to ascertain the genealogical depth of parents is the name of the extended family from which a wife derives.

Method Of "F" Computation

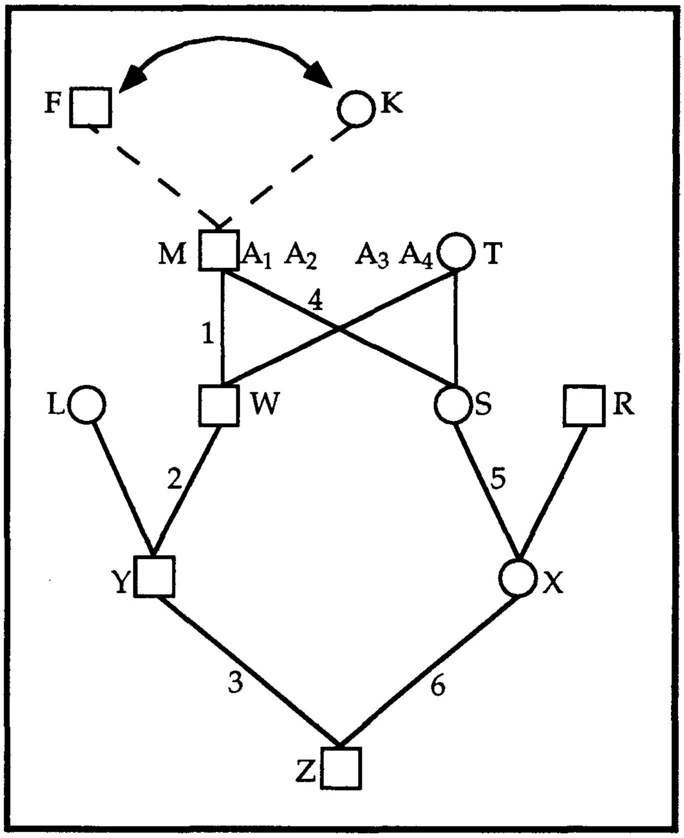
Path Analysis

This technique, first proposed by Wright (1921), enables one to compute a coefficient of inbreeding, once we know the biological relationships between parents. This coefficient is the correlation between uniting gametes and is computed by assigning a value of 1 to gene "A" and a value of zero to its allele "a" (or, in fact, any arbitrary value). The correlation is usually designated by "F" or "f". According to Wright's model, if n and n' are the number of generations in the pathway tracing back to a common ancestor of both parents of individual Z, then:

$$F=\sum_{i=1}^{n} (1/2)^{n'+n+1}$$

The idea behind this system is illustrated in Fig. 12. Here we can see the links of the descendant (Z) to earlier common generations. When both parents are first cousins, the probability that gene A1 will get to descendant Z via the parents in pathways 1, 2 and 3 is $(1/2)^3$. The same probability exists also for pathways 4, 5 and 6. Hence the probability that descendant Z will be homozygous for gene A1 is $[(1/2)^3 \times (1/2)^3] = 1/64$. The probability that he will be homozygous for one of the four genes represented in the autosomal locus of the parents will therefore be: $4 \times 1/64 = 1/16$. In societies where there is a long chain of arranged marriages tracing back to a depth of many generations, it is possible that in individual M the A1 gene is already in the homozygous state. Consequently, in every calculation of F, one needs to take into account also the F values of the preceding generations. The fact that M himself in Fig. 12 is already a product of a long line of marriages within very small groups, increases the probability that S and W will receive genes which are identical by origin from M by a factor of $F_A/2$. Therefore all the marital loops linked to a common ancestor require multiplication by a factor of $1+F_A$*.

FIGURE 12: Genealogy of Inbred Individuals Originating from One Family (mates F and K)



The Contribution of Marital Patterns in the Tribe to the F Value in the Present Generation

We recognized five different Fxe_i's in the South Sinai Bedouin, one for each conjugal type, thus: Fxe_1 for marriages within the Hams (blood feud group); Fxe_2 for marriages within the extended family; Fxe_3 for marriages within the clan; Fxe_4 for marriages within the sub-tribe; Fxe_5 for marriages within the tribe. On the basis of the structuring of marital patterns in the tribe, we computed for each Fxe_i the genealogical distance, in generations, between the parents and their common ancestor.

The genealogical depth of the Muzeina tribe is estimated to be about 16 generations. We further assumed that the parental pairs on which there is no genealogical information, distribute proportionally into our five recognized marital categories; these comprise about 4.4% in the 15 generation according to the Hams blood feud group records (see Table 9). The computation of the suitable Fxe_i was done according to the formula:

$$Fxe_i=PFxe_i+\sum_{i=1}^{n}[(1/2)^{n'+n+1}]/100-u$$

where P is the proportion of the particular marital pattern within the total marital patterns in the sample, and u is the percentage of cases per generation of parent pairs for which no adequate genealogical data were available to us. The final value of Fxe is obtained by combining all the computed Fxei values:

$$\overline{Fxe} = \sum_{i=1}^{5} Fxe_i$$

(The data on which the computations were made are given in Table 9.)

Computation of Various Fxe_i

Marriages within the Hams (blood feud group) (Fxe_1).

This category includes four main marital types. Marriages between first cousins are marriages to the children of the father's brother or those of the mother's sister. Of the total marriages within the blood feud group recorded from our genealogical trees (for the Muzeina only), 58.5% were marriages with offspring of the father's brother and only 18.8% with offspring of the mother's sister. This datum reflects the trend of cousins for marrying the children of the father's brother, but is not entirely free of error because the Bedouins are reticent about reporting marriages with the offspring of the mother's sister as marriages between cousins. For the same reason, there is in fact some question about the true marital rate of first cousins within the tribe. According to the studied genealogical trees, first-cousin marriages (of both types) probably do comprise about 77.3% of all marriages in the Hams. Second-cousin marriages account for about 15.1%, and third-cousin marriages some 2.0%. Marriages between relatives of two different generations are about 5.6%. It should be noted that the greater the genealogical depth, the greater the error in the estimates of the frequency rates of the marital types.

The contribution of different marital types within the Muzeina and their frequencies within the population to the Fxe_i value are: First-cousin marriages: $(1/2)^5 x0.773 = 0.024156$; Second-cousin marriages: $(1/2)^7 x0.151=0.001179$; Third-cousin marriages: $(1/2)^9 x0.02=0.00003906$; Cross-generational (uncle-niece) marriages between relatives: $(1/2)^6 x0.056= 0.0008749$, with a combined value of 0.026248.

Since in the Muzeina tribe marriages within the Hams are only 14.6% of all marriages, the relative contribution of this marital pattern to the F value of the population is $Fxe_1 = 0.026264x0.146 = 0.003834$.

Marriages within the extended family (Fxe_2).

The common genealogical depth for a pair of parents extends to 6-7 generations. We elected to use the latter datum albeit significantly reducing the obtained F values. The frequency of this marital type accounts for 20.4% in the 15 (parent) generation (Table 9). Thus, $Fxe_2 = (1/2)^{13} x\ 0.204 = 0.0000249$

Marriages at the clan level (Fxe_3).

The genealogical depth here is 8-9 generations and the frequency of this marital type is 33.7% (Table 9) . Hence, $Fxe_3 = (1/2)^{17} x\ 0.337 = 0.0000026$

Marriages within the sub-tribe (Fxe_4).

The genealogical depth amounts to 10-12 generations: frequency 8.5%. Thus: $Fxe_4 = (1/2)^{21}$ x 0.085 = 4.0531-08

Marriages within the tribe (Fxe_5).

The genealogical depth exceeds 12+ generations: mean frequency is 15%. Hence, $Fxe_5 = (1/2)^{25} x\ 0.15$ = 4.4703-09

Overall Contribution of Marital Patterns to Coefficient of Inbreeding (Fxe) in the Parent (fifteen) Generation

The overall value of $F\bar{x}e_{1-5}$ obtained by us (0.0038615) comprises almost entirely (96.3%) the effect of first-cousin marriages. The contribution of all the other marital patterns to the value of $F\bar{x}e$ is negligible (3.7%). All these $F\bar{x}e$ values refer of course to one generation only, for when inbreeding processes are allowed to carry into a greater depth of generations the contribution of the other marital patterns to the overall $F\bar{x}e$ value also increases. It may be noted that the obtained value is probably lower than the true value owing to the probability of inaccurate information provided on cousin marriages with offspring of the mother's sister, as previously observed.

Contribution of Tribal Marriage Patterns in Earlier Generations to Value of Fxe

The use made of the Hams (blood feud group) records to compute the Fxe for earlier generations poses two main problems:

a)The deeper one delves into early generations (i.e., 1st, 2nd...,15th generation), the smaller the value of the expression n'+n+1, the latter indicating the number of individuals participating in the inbreeding loop linking all the common ancestors of individual Z. Therefore, the composition of the tribe, as described in the present study (Fig. 3) indicates a fixed situation for a given unit of time. The further back we proceed in the number of generations, the more distorted becomes the structure of the tribe as we recognize it, and the marital patterns may assume a genealogy entirely different from that shown in Fig. 3.

b)The frequencies of the different marital types are, inter alia, a function of group size. In a sample of 60 cases of cousin marriages within the Muzeina tribe, we found that 53% occurred in blood feud groups numbering in excess of 60 individuals, 31.6% in blood feud groups of 40-60 individuals and only 15% in blood feud groups of up to 40 individuals. Furthermore, in blood feud groups of less than 30 individuals cousin marriages were extremely rare. There is a clear correlation between Hams (blood feud groups) size and frequency of cousin marriages, but demographic reconstruction of the past history of the Hams did not enable us to evaluate fluctuations in population size or in the Hams size and therefore we must assume a fixed mean growth rate for all earlier generations. Consequently, we will consider the number of individuals in the Hams, in each generation, as stable, and the rates of marriages between cousins will be also estimated as stable since the number of cousins for each individual remains fixed in every generation.

In order to optimally compute the overall coefficient of inbreeding for the South Sinai Bedouin society (F), after 15 generations, we took into account the following possible variables:

Fxi = the inbreeding coefficient per generation.

Fxe = contribution of the breeding patterns to the coefficient of inbreeding.

Fin = the influence of the genetic drift (depending on size of the Ne).

Our final working formula, based on Li (1968) became:

$F = [Fxi_{16}(1+F_A)] \times (1-M)^2$

There are three main parameters which contribute to a determination of the F value. These are: the inbreeding coefficient for the present generation (Fxi_{16}); the contribution of earlier generations to the final inbreeding coefficient ($1+F_A$) and the effect of immigration during the last generation $(1-M)^2$. The estimated F value is **0.09802**. It is noteworthy that both Fxi_{16} and F_A include the following variables: breeding patterns; genetic drift; differential fertility; and the sex ratio and extent of polygamy. The computation procedure for F can be found in Appendix 2.

Imigration rates affecting the F value in South Sinai Bedouins

Since the tribe is the biosocial unit with which we are primarily concerned, it was deemed worthwhile to ascertain the effect which an average 3% migration rate per generation would have on the F value. The formula chosen for this purpose (after Li, 1968, p.305) takes into account both the effect of inbreeding as well as that of genetic drift (formula 8). Thus, the F value for the entire Muzeina tribe, when Ne=846 and the migration rate is 3%, will be:

$F = (1-M)^2/[2Ne-(2Ne-1)(1-M)^2]=(1-0.03)^2/[1692-(1692-1)(1-0.03)^2]= 0.009315$

The value of F for groups of related sub-tribes (super sub-tribes) that have a common ancestor within the Muzeina tribe, when Ne=564 and the migration rate is 6%, would then be: F = 0.00684.

And similarly, the value of F for the sub-tribal framework (Ne=141, migration rate = 23%) would be: F =0.005137.

The largest F value obtained was for the tribal framework. Hence, we shall employ the tribal framework as the intersocial unit. Yet the fact that the F values for the other two frameworks are not much lower also suggests other possibilities. The relationships between the migration rate on the one hand, and the effective size of the population on the other, are such that a rise in heterozygosity within the first two sub-units, namely, the sub-tribe and the super-sub-tribe (stemming from an increased migration rate) is greater than the rise in homozygosity within the same groups, owing to reduction in their effective size.

Summary

The discrepancy between the value of F for the 16th generation only (F_{16} = 0.004297) and the one obtained for all generations together (F_{1-16}=0.09802) illustrates why F values computed for different human societies are relatively small. Up to the early 1970's, the highest F value computed for a human population (F=0.043) was that for the Samaritans by Bonne' (1963). Numerous studies (e.g. Salzano, 1972, on nine tribes of American Indians and Eskimo populations) along the same line have led investigators to the conclusion that this value (0.043) was about the upper limit of F possible in human populations. Subsequently, however, it was found that the upper limit can be somewhat higher (F=0.050; Katayama et al., 1981). Among the many studies of the topic, the one by Spielman et al. (1975) is especially relevant to our present study, for the values computed by those investigators for American Indian populations took into account past biological processes. Spielman and his associates noted that in such a computation the value of F can turn out to be much higher than one might suppose. According to these authors:

> *...it is difficult to escape the conclusion that except at loci with very high heterozygosity maintained by selection, identity by descent from ancestral alleles in Amerindians founders for a pair of randomly chosen alleles in a contemporary Amerindian tribe should be no less than* ***0.3*** *and may well be greater than* ***0.5*** (p.367).

Their value is manifestly higher than obtained by us, but if we take into account that the duration of the formation of Indian societies in America is vastly longer than that of the Bedouin tribes in the Sinai, the higher value is understandable.

Genetic Composition And F Values In The Bedouin Society Vis-A-Vis The Known Gene Frequency

Here we shall attempt to ascertain the high value of F in the South Sinai Bedouin society on the basis of the evidence available pertaining to the various gene frequencies.

Mathematical manipulations in population genetics usually presuppose that the entire population is a single panmictic unit, that is, that the choice of a mate from among the total population is a random process. This assumption, however, as noted in the preceding (see chapter on Marital Patterns), is inapplicable for the South Sinai Bedouins as well as indeed for much larger populations since they generally split up into a number of sub-populations due to various factors such as geographic location, topographic barriers, religion, economic status, etc. (Wahlund, 1928).

The first important contribution to a mathematical consideration of a "splitting" in populations insofar as a local differentiation of gene frequency is concerned, was made by Wright (1940, 1943, 1951). Wright developed a series of F coefficients for split populations and demonstrated their interrelations (Wright, 1965). Assuming that a total population (T) is divided into isolated sub-populations (S), the inbreeding coefficient for individual "I" comparable to the total population (T) is obtainable from the formula $F_{IT} = F_{ST} + (1-F_{ST})F_{IS}$ (Kimura and Ohta, 1971, p.118) where F_{IS} is the inbreeding coefficient for the individual relative to the sub-population to which he belongs and F_{ST} is the inbreeding coefficient of his sub-population relative to the total population. Thus F_{ST} is the correlate between random gametes taken from the same sub-population. In terms of a panmictic index, P=1-F, the relationships can also be expressed by: $P_{IT}= (P_{IS} \times P_{ST})$. (Kimura and Ohta, 1971, p.118) Because the inbreeding coefficient can be interpreted as the probability that two homologous genes in united gametes are the result of a common ancestry (Malecot, 1948), it is important to derive the formula in reference to such a probability. Crow and Kimura (1970) have indicated that the term P_{IT} (or $1-F_{IT}$) represents the overall probability that two homologous genes in individual I are <u>not</u> identical owing to a derivation from a common ancestor. The term P_{IT} is equal to the product of the two probabilities P_{IS} and P_{ST}, the first of which is the probability that two homologous genes in individual I are not identical by origin relative to the number of sub-populations (S). The second is the probability that two homologous genes picked at random from a sub-population S are not identical by origin. From these definitions it is clear that F_{IS} reflects the influence of local matings (such as consanguineous marriages) within sub-populations S, whereas F_{ST} reflects the influence of a genetic drift on the differentiation in the gene frequency among sub-populations.

It should be noted that F_{ST} will never equal zero even were matings in each sub-population to be completely random.

The inbreeding coefficient is readily computable if we know the frequencies of the various genes in the sub-populations. According to Wright (1943), if the mean and variance of the frequencies of a given allele in the sub-populations are $\overline{P}$ and S_p^2, respectively, then $F_{ST}=S_p^2/[\overline{\overline{P}(1-\overline{P})}]$ (Kimura and Ohta, 1971, p.120).

This formula of Wright's was subsequently broadened by Nei (1965) to encompass also systems of multiple alleles, as follows: $F_{ST}=-S_{jk}/\overline{P}_j\overline{P}_k$ where S_{jk} is the covariance of the frequencies of the alleles k and j while $\overline{P}_j$ and $\overline{P}_k^{jk}$ are the mean frequencies.

The application of these formulas to the Bedouin population of South Sinai is dependent on two requisites: a)that all the tribes under consideration be derived from the same population; and b)that we have on hand reliable data on gene frequencies in each tribe.

The first condition or requisite holds true for some of the Bedouin tribes, that is, for the tribes that derive from Saudi Arabia (see chapter on "History of the South Sinai Tribes"). The second condition is also fulfilled albeit the quantity of data available is limited and based mainly on the studies of others: Kaufman-Zivelin, (1971) on types of haptoglobins and transferins in the Bedouin population of South Sinai; Bonne' et al. (1971) on heritable blood factors; and Ben-David (Kobyliansky) et al. (1982) on the sensitivity to Phenylthiocarbamide (PTC) tasting among South Sinai Bedouins.

We could calculate the F_{ST} values between two tribes, the Muzeina and Aleigat, for two systems, namely, the P (blood group) and the Hp (haptoglobins). Also calculable for four tribes (Muzeina, Aleigat, Gararsha and Awlad Said) are the F_{ST} values for an additional system, the T (Phenylthiocarbamide); and for two tribes (Muzeina and Aleigat) we could calculate the F_{ST} values for a multiple allele system, namely, the ABO blood group.

a. Comparison of the blood group P

The genetic marker P represents one of the blood groups. It is a two-allele gene (P_1 and P_2) of which the P_2 is dominant. Computation of the F_{ST} for the frequency of this gene is given below.

F_{ST} value between the Muzeina and Aleigat tribes for system P (blood group):

Gene	Muzeina	Aleigat	$\overline{X}$	S.D.	F_{St}
P_1	0.572	0.366	0.469	0.146	0.085

b. Comparison of the frequency of the Hp1 gene

The haptoglobins (Hp) are glycoproteins present in the serum which are capable of binding hemoglobin (Hb). All the haptoglobin types designated Hp1-1, Hp2-1 and Hp2-2 derive from a pair of autosomal alleles Hp1 and Hp2. The F_{ST} computed from these is given below.

F_{ST} value between the Muzeina and Aleigat tribes for system Hp1 (haptoglobins):

Gene	Muzeina	Aleigat	$\bar{X}$	S.D.	F_{St}
Hp1	0.280	0.510	0.395	0.163	0.111

c. Comparison of the T gene frequency (sensitivity to phenylthiocarbamide)

In the case of the T gene we had data from two additional Bedouin tribes (Awlad Said and Gararsha) whose origin was close to that of the first two (Muzeina and Aleigat), and therefore we could compute the F_{ST} of four tribes .

F_{ST} value between the Muzeina, Aleigat, Awlad Said and Gararsha tribes, for system T (phenylthiocarbamide):

Gene	Muzeina	Aleigat	Awlad Said	Gararsha	$\bar{X}$	S.D.	F_{St}
T	0.354	0.248	0.458	0.178	0.317	0.136	0.085

d. Comparison of the gene frequency in the ABO system

Since definite identification of the phenotype A intermediate is questionable, we resorted to three alleles only, namely, p, q and r. The various computations were made from the formula of Nei (1965) for a multiple allele system. Owing to the complexity of the system and of the computation technique, which differs slightly among investigators, we have used the method of Thoma (1970).

For systems of single alleles (P_1, Hp1, T) we computed the χ^2 values from the test of Snedecor and Irwin (1933). Thus $\chi^2 = (\bar{p}-p_i)^2 2n_i/\bar{p}(1-p)$ where p_i = the frequency of the gene in a given group, $\bar{p}$ = the mean i weighted frequency of the same gene, and n = size of the sample.

For the multiple allele system (ABO) we computed the χ values from the formula by Thoma (1970): $\chi^2_{(k-1)} \cong KV^{o}_{p} \cong V'p$

The χ^2 values obtained for single allele systems all show significant differences between the Muzeina and Aleigat tribes for P_1 and Hp1, and between the Muzeina, Aleigat, Awlad Said and Gararsha tribes for T (Table 18). The values obtained for the multiple allele ABO system are given in Table 19.

TABLE 18 Intertribal differences in frequencies of genes P1, Hp1 and T by the χ^2 method.

System	P1	Hp1	T
c^2	14.34	23.37	24.58
P	<0.001	<0.001	<0.001

TABLE 19 Differences in the ABO system between the Muzeina and Aleigat tribes.

	Gene		
	(p)	(q)	(r)
Muzeina	0.171	0.132	0.698
Aleigat	0.198	0.124	0.678
$\overline{X}$	0.185	0.128	0.688
n	107	107	107
V^0	0.0001793	0.000016	0.00010
V'	0.0007812	0.000559	0.00112
V	-0.0006091	-0.000543	-0.00102

Since all the observed genetic variances (V^0) between the Muzeina and Aleigat tribes are significantly smaller than the sampling variances (V'), it is clearly pointless to compute the χ^2 values, for the common variances and the different F_{ST} values. Thus we are in a situation where, in the single allele systems, there is a significant difference between the tribes while in the multiple allele system there is no significant difference. Perhaps the difficulty here stems from the fact that we have chosen to use the ABO system which is known to be a problematic one in identifying differences between ethnic groups (Kobyliansky and Livshits, 1983). Yet, on the basis of the results obtained with the systems of single alleles, we can pose the question: "What are the factors leading to differences in gene frequencies between tribes?" There are two possible answers to this question, namely: (a)genetic drift, and (b)selection.

To ascertain which of these two alternatives was applicable in our case, we examined the relationship between the observed variance and the expected variance with regard to the inbreeding coefficient F_{ST}. We reasoned that if the observed variance is greater than the expected, then it is probably selection which acted to bring about the intertribal differences in allele frequencies because only selective forces could throw the system out of balance. On the other hand, if we find that the observed is less than the expected, we must attribute the difference in gene frequencies among the tribes to random processes, such as genetic drift.

Our results show that the observed variance of F is $S^2_{obs.}= 0.0002176$, whereas the expected variance of F was $S^2_{exp.}= 0.005836$. The computation was by the formula $S^2_{exp.}=2\overline{F}^2_{ST}/(n-1)$, where F_{ST}= the mean F value for the three systems and n-1= number of populations (according to Lewontin and Krakauer, 1973). The ratio $S^2obs./S^2exp.$ amounted to 0.037285. Insofar as this ratio showed the same distribution as did the ratio χ^2/df (Lewontin and Krakauer, 1973), we computed the corresponding value (0.037285) for the χ^2 distribution (26.82). It was statistically significant ($p<0.001$), which indicated that the observed ($S^2_{obs.}$) heterogeneity was significantly lower than the expected heterogeneity ($S^2_{exp.}$). Consequently we may conclude that differences in gene frequencies among the tribes are probably due to random processes, and that the selection factor is little if at all responsible for the intertribal differences. Hence, perhaps we should not expect to find in it adaptive differentiation among the Bedouin in its various zones. It seems reasonable to assume that any selective pressures would be virtually identical for all the sub-groups in South Sinai. Li (1968) and Thoma (1970) report that an adaptive differentiation can only occur in broad geographic regions, such as the various European countries. Yet, Kobyliansky and Livshits (1983) have shown that in small, isolated Jewish groups such as the Samaritans, the Karaites or the Habbanites, selection was the main factor responsible for differences in their gene frequencies, of the ABO system. But these groups differ from the Bedouin tribes in that the former are small groups originally geographically very remote from one another, e.g., the Samaritans in Israel, Karaites in Iraq, and the Habbanites in Hadramaut (a costal region of South Arabia), each also very different in environment and socio-economic circumstances. In short, they are not a suitable model for comparison with the Bedouins of South Sinai.

Population genetic structure models: their implementation to the south Sinai Bedouins.

To gain insight on the link between social and genetic components in the South Sinai Bedouin population, we could have employed existing models in the literature, but none of them appeared applicable to the Bedouin society.

The two main models for the study of population structure, proposed by Wright (1951), are known as the "Island Model" and the "Isolation by Distance".

In the former, the general population is comprised of a series of sub-groups with an effective size (Ne) in each of which the matings are random. This model assumes that individuals in the population are replaced as a single unit at a rate of M per generation and that the migrants stem randomly from the general population without any tendency for them to come from neighboring groups. The second model assumes that the general population distributes uniformly over a wide territory, with the parents of each individual surveyed being taken at random from a limited geographic area. The main variable in the latter model is "Size of Neighborhood" which is in fact the effective size of the population in the specific area from which the parents came (Mn).

In view of our knowledge of the Bedouin of the South Sinai region (see chapter on Ethnography), it is clear to us that the prerequisites for the use of one or the other of Wright's two models are not fulfilled. Models similar to those of Wright have been suggested by Malecot (1948, 1967). In his model one would expect that individuals living adjacently will be more similar genetically than individuals living far apart. The main parameter in Malecot's model is the "Coefficient of Kinship", which is the probability that two homologous genes, picked at random, from two different individuals, will be identical by descent. As we have seen, geographic distance is not always the leading factor in the selection of a mate among adjacent bedouin tribes (although it does in certain cases), but rather the historical relationship plays a much more important role. Consequently the model of Malecot is also not applicable here.

Another model for the study of populations has been proposed by Kimura (1953), namely, the "Stepping-stone Model". This model, in which the general population is divided into a number of separate population units (similarly to the "Island Model"), is actually an amalgamation of the two models proposed by Wright, but the exchange of individuals takes place only between adjacent settlements. Kimura and his associates added further mathematical elaborations to their basic model (Kimura and Weiss, 1964; Weiss and Kimura, 1965), but even these do not render their model suitable for our Bedouin population study.

Thus, to illustrate the problems or difficulties in using such a model as the "stepping-stone" for the Bedouin society, let us take the simple case of the one-dimensional "stepping-stone" with a finite number of groups arranged linearly. The Muzeina tribe is adjacent to both the Aleigat and the Gebeliya tribes. By the "stepping-stone" model, the Muzeina tribe should exchange individuals with the other two tribes at a rate of M_1 per generation, so that $M_1/2$ will be the proportion of exchanged individuals between adjacent tribal pairs per generation unit. The trouble is, however, that in Bedouin society there is not always a connection between geographic proximity and exchanges of population, as indicated previously.

Neither do improved models of the "stepping-stone" type, such as that by Maruyama (1970), known as the "Circular stepping-stone Model", suit the purposes of the present study.

Effect of inbreeding on population demography and child development

a. Survival Factors (Fertility and Mortality)

Having computed F (0.09802) for the South Sinai Bedouin, we next attempt to learn, from the data available in the literature, what may be the direct and/or indirect influence of such an F value on the health of the population.

Schull (1972) distinguishes between the influence of inbreeding (the effects on offspring number and kind which results from a parent being the product of a consanguineous marriage) and consanguinity (the effect of consanguineous marriage on the number and kind of offspring born to such a marriage) in a population. Based on a previous extensive study involving more that 10,000 families in Japan (Schull et al., 1970), Schull writes (1972):

> *No effect of paternal inbreeding was observed, but neither parental inbreeding nor consanguinity could be shown to exert a significant effect upon the frequency of stillbirths* (p.158).

Yet, in an earlier study (Schull and Neel, 1965), it was found that the risk of death or disease was greater among the children of consanguineous marriages than among children whose parents were not related.

Findings regarding fertility are more clear-cut, for here the overall number of pregnancies and of newborns increased significantly with consanguinity (Schull, 1972). However, the "net fertility" (i.e., total live births minus non-accidental deaths prior to age 21) does not increase significantly if one takes into account factors such as socio-economic status and religious affiliation of the parents. Quoting from studies carried out on various Japanese populations, Schull (1972) summarizes the topic of mortality and inbreeding (consanguinity) as:

> *...mortality in the first twenty years of life increases about 0.5 percent per percentage foetal inbreeding (consanguinity), and by a lesser amount as a function of maternal inbreeding* (p.158).

b. child development

The influence of consanguinity and parental inbreeding on behavioral and constitutional traits of child development, has been studied first on Japanese groups (Schull and Neel 1965; Neel et al., 1970a,b).

Results of these studies have failed to show:

> *...any clear effect of parental inbreeding on such diverse indicators of possible effects as physical development, systolic and diastolic blood pressure.......eye and ear diseases, visual accommodation, visual and auditory acuity, intelligence, school performance* (Schull, 1972 p. 158).

On the other hand, consanguinity was found to have some influence on child growth and development, albeit minor and only in some respects. Thus Schull (1972) wrote:

> *...all of the metrics of physical and mental growth and development were depressed with consanguinity. The effects, though demonstrated, were small, amounting to at most a few percent of the mean of the outbred children* (pp.158-159).

It may be noted that the effect of inbreeding has been evaluated in many controlled experiments on animals. Spuhler (1972) may be cited in this regard:

> *...the two most important observed consequences of inbreeding in experimental and farm animals are (1)the reduction of the mean phenotypic value shown by characters connected with reproductive capacity or physiological efficiency, and (2)the increase in uniformity, or reduction in variance, about the mean phenotypic values within an inbred line* (p.166).

Food support received by South Sinai Bedouin From Welfare agency