

APPENDIX 1:

Computation Methods of Population Effective Size

Two alternative methods of computing the overall effective size for the last generation (Ne_{16}) in the Muzeina tribe are here presented. Three different parameters were taken into consideration: Ne_s = the effect of sex ratio on Ne size; Ne_p = the effect of polygamy; and Ne_m = the effect of migration.

Method A

$$Ne_{16} = Ne_1 + Ne_2$$

When Ne_1 takes into account the effect of polygamy on Ne :

$$[1/8 Ne_p = (3/32 N_f + 1/32 N_m)]$$

in proportion to its frequency (f_p) in the tribe:

$$(Ne_1 = Ne_p \times f_p),$$

and where Ne_2 takes into account the sex ratio in the population:

$$([1/Ne_s = 1/4 N_f + 1/4 N_m])$$

in proportion to the percentage of monogamy ($100-f_p$) in the tribe:

$$Ne_2 = Ne_s \times (100-f_p).$$

Next we subtract the influence of immigration on the Ne :

$$Ne_m = Ne_{16} \times (1-m)^2.$$

The value of Ne_m is the effective size of the population with which we shall deal hereafter.

For the Muzeina tribe, we have the following data:

The sex ratio: $N_m/N_f=106.9$; the population size: $N_{16}=3000$; polygamy rate: $p=12.1\%$; migration rate: $m=3\%$.

Normally, in a population of 3000 individuals, 1000 will be in their reproductive period. Considering the sex ratio (106.9), this group is composed of 515 males and 485 females.

Interpolation of these data into the formula yields for polygamy:

$$1/8 N_{ep} = 3/16,480 + 1/15,520 = 507.23$$

$$N_{e1} = 507.23 \times 0.12 = 60.86;$$

for the sex ratio:

$$1/N_{es} = 1/4 (1/515 + 1/485) = 999.11$$

$$N_{e2} = 999.11 \times 0.88 = 879.21;$$

$$N_{e'} = 60.86 + 879.21 = 940.07;$$

and for migration rate:

$$N_{em} = 940.07 \times (1-0.03)^2 = 884.51$$

Method B

Let us use the formula for differential fertility in such a manner that the polygamy problem will be indirectly bypassed. We shall compute the N_e from the two components N_{em} and N_{ef} (see chapter on "Factors which affect the genetic composition of the Bedouin tribes".) Clearly in a polygamous society, where there are probably more mothers than fathers, the values of vtw (variance in number of children per mother) and vtt (variance in number of children per father) will not be identical. After we obtain the values of N_{em} and N_{ef} we shall compute the N_e from the sex ratio formula. We should mention that the sex ratio must be used whenever N_e is computed since changes in the sex ratio diminish the heterogeneity of the population proportional to it.

For the Muzeina tribe we have the data:

sex ratio = 106.9; the effective population size $N_e = 1000$.

$k_w = 3.06$ $v_{tw} = 4.19$

$k_t = 3.83$ $v_{tt} = 7.42$

$$N_{em} = \frac{N m k_t - 2}{k_t - 1 + v_{tt} / k_t}$$

$$N_{ef} = \frac{N f k_w - 2}{k_w - 1 + v_{tw} / k_w}$$

$$N_{em} = 423.17$$

$$N_{ef} = 422.43$$

Where k_w and k_t are the mean number of children per mother and father, respectively, N_{em} and N_{ef} are the estimated number of males and females, respectively, in relation to the effective size (N_e) of the tribe in the 16th generation. The values obtained for N_{em} and N_{ef} enable computation of the N_e in the following way:

$$1/N_e = 1/4 (1/423 + 1/422);$$

$$N_e = 846.15.$$

The difference between the value of the N_e obtained by the first method and that obtained by the second is relatively minor, having only marginal effect on the fixation index (influence of genetic drift).

APPENDIX 2:

Stages of Coefficient of Inbreeding (F) Computation in the Bedouin Population based on Muzeina data:

Computing $F_{xi_{16}}$

A. We compute F_{xe_i} for the tribe in the last generation as related to breeding patterns only:

$$1. F_{xe_i} = \sum_{i=16}^{16} \left[\frac{1}{2}^{n'+n+1} \right]$$

The mean result obtained is 0.003978.

B. We compute the effect of genetic drift during the last generation. In determining N_e we elected to use the result obtained by the second method (see Appendix 1), which is based mainly on the differential fertility and sex ratio formulas.

C. We compute F_{xi} for the 16th generation:

$$2. F_{xi_{16}} = 1/2N_e + [(2N_e-1)/2N_e \times F_{xe_i}] = 0.004566$$

Computing FA

The computation of FA, the contribution of the previous generations to the the F level, is problematic owing to the uncertainty which exists regarding the biological processes occurring in early generations. Hence, most investigators prefer to ignore this factor. However, in the present case it is mandatory to consider the FA because of the considerable effect it may exert on the final value of F. Ideally, the computation is done by the following formula:

$$3. FA_{15} = 1 - (1 - \Delta F)^{15}$$

$$4. \Delta F = (1 - M)^2 \times [1/2\overline{N_e} + [(2\overline{N_e}-1)/2\overline{N_e}] \times \overline{F_{xe}}]$$

$$5. 1/\overline{N_e} = 1/(t-1) \times [1/2N_{e1} + 1/2N_{e2} + \dots + 1/2N_{et-1}]$$

$$6. \overline{F_{xe}} = \sum_{i=1}^{16} \left[\frac{1}{2}^{n'+n+1} \right] 15$$

In as much as various factors (e.g. M = immigration rate, N_e = effective size, F_{xe} = breeding patterns, t = number of previous generations to common ancestor) exert a differential effect on F , we discuss each separately and show the necessary steps in their computation.

Computation of the different variables (M , N_e , F_{xe})

Immigration rate (M): In the last three generations the immigration rate in the Muzeina tribe ranged between 2-4%. We have no information on immigration rates in earlier generations and therefore perforce must use the mean value of the immigration rates in the last three generations (3%) as a constant for all the tribal generations except the first five. Since the mean size of the Hams (blood feud group) starting from the 6th generation will thus remain constant (see below), the number of possible consanguineous marriages per generation will also remain constant.

Effective size (N_e): Computing the average weight or effect which genetic drift exerts on the F value in the Muzeina tribe was done in several stages: a) we calculate the rate of natural increase (P), the rate of population growth (r) and the doubling time (Dt) for previous generations; b) we calculated the population size per generation to a depth of 16 generations; c) we took a third of the population size and computed the breeding size of the population per generation; d) we computed the effect of differential fertility and sex ratio on the breeding size of each generation and on the effective size.

Coefficient of inbreeding (F_{xe}): The simple and easy way to achieve a partial solution of the problem would seemingly be to compute the coefficient of correlation between the group size and the frequency of the various breeding patterns, with emphasis on first-cousin marriages, and then construct a regression equation and use it to predict the F_{xe} values for the various generations. This system, however, has two main drawbacks. First, there is no linear correlation between the two variables and second, even more important, the structure of Bedouin society is such that the number of individuals in the Hams (blood feud group) after the first five generations (from the tribe's foundation) remains more or less constant regardless of the number of generations. Having assumed that neither the mean number of children per family nor the sex ratio changed in the last generations, we may justifiably argue that the number of first cousins in each generation remains fairly constant as well. What does vary is the number of second, third and fourth cousins who,

however, as previously shown, exert little influence on the \overline{Fxe} . The number of blood feud groups in each generation will increase and so also will the tribe, but the mean number of individuals per blood feud group, regardless of generation, will remain more or less constant.

Method of computation. On the basis of the preceding, it is clear that the computation of \overline{Fxe} is to be made for two periods of genealogical time: the first extending from the founder's generation to the 5th generation, and the second, from the 6th generation to the penultimate one, that is the generation of children examined by us (G5 in Hams records). Hence the computation of \overline{Fxi} for the last 10 generations is:

$$\overline{Fxi}_{6-15} = 1/2\overline{Ne}_{6-15} + [(2\overline{Ne}_{6-15}-1)/2\overline{Ne}_{6-15}] \times \overline{Fxe}$$

and computation of \overline{Ne} for the last 10 generations yields: $\overline{Ne}_{6-15} = 113.63$.

Therefore the mean effect per generation of the genetic drift on the \overline{Fxi}_{6-15} will be:

$$\overline{Fin}_{6-15} = 1/2\overline{Ne}_{6-15}$$

$$\overline{Fin}_{6-15} = 0.0044$$

The effect of the breeding patterns on \overline{Fxi}_{6-15} is estimated only on the basis of first cousins, since: 1) each individual in each of the 10 generations has, on average, an identical number of first cousins; 2) the relative contribution of this breeding pattern (from the overall contribution which marital patterns have) in determining the value of \overline{Fxe} exceeds 95% and therefore it is unnecessary to compute all the components of the breeding patterns, in this case $\overline{Fxe} = \overline{Fxe}_1$; and 3) since the number of first cousins per individual is identical in all generations, we can employ the rate of first-cousin marriages which was determined for the blood feud groups, with the 16th generation taken as a constant for the other 10 generations (6-15). Thus:

$$\overline{Fxi}_{6-15} = [(2\overline{Ne}_{6-15}-1)/2\overline{Ne}_{6-15}] \times \overline{Fxe}$$

$$\overline{Fxi}_{6-15} = 0.9556 \times 0.003834 = 0.003817$$

Now we can compute the mean value of F for the last 10 generations thus:

$$F_{6-15} = (0.0044 + 0.003817 \times (1-0.03)^2) = 0.007731$$

And from this, to compute the FA_{6-15} :

$$FA_{6-15} = 1 - (1 - F)^{10} = 0.07468$$

Determining the contribution of the first five generations to the overall coefficient of inbreeding (F) of the tribe is problematic mainly because the social frameworks in the tribe during this period are not yet consolidated. And in the absence of any guiding principle to follow its social development, we must inspect each generation and learn its possible behavior, with respect to marital patterns, migration, etc., and then try to evaluate the overall contribution of these generations to the overall coefficient of inbreeding (F).

As a rule one can continue to compute the N_e for the first five generations in the same way it was done for the later generations. However, we must exclude the first generation since it is responsible for introducing the primary genetic background into the group. Our computation of the average effective size for the first five generations therefore becomes:

$$\overline{N_{e1-5}} = 22.49$$

and the mean effect per generation of the genetic drift on the F_{xi1-5} will be:

$$F_{in} = 1/2N_{e1-5} = 0.0222.$$

Computing immigration rate (M) for the first five generations.

The potential for consanguineous marriages is largely reduced in the first generations mainly because of the small tribal size, ranging from 46 individuals in the first generation to 187 in the sixth. Therefore, it is clear that many individuals in the first generations will take brides who are outside their Hams (blood feud group). Since the Hams is patrilineal in nature, all the males will always be of the same tribe, while the females can be either from inside or from outside the group. The role of immigration is therefore expected to increase, and can be estimated from the size of the tribe in those generation in which that value is similar to the size of the extended family or clan in the present generation. Since 68.7% of marriages are within the clan, the average rate of immigration for generations 4 and 5 is 32%, whereas for generations 1, 2 and 3 (extended family) it is 65%. Thus, the average migration rate for generations 1-5

is approximately 48%. The effective size of the group in the first generations is small, and hence, the influence of genetic drift may mask the impact of inbreeding. And since the fixation of genes cannot act twice, that is, once under the effect of genetic drift and again under the effect of breeding patterns, one cannot use breeding patterns in the first to fifth generations as a component in the final value of FA_{1-5} . Therefore, the influence of breeding patterns for the first five generations must be computed thus:

$$F_{1-5} = (1/2\overline{Ne}_{1-5}) \times (1-M)^2 = 0.022 \times 0.27 = 0.00594$$

and the FA_{1-5} computation is:

$$FA_{1-5} = 1 - (1 - 0.00594)^4 = 0.0236$$

After calculating the inbreeding coefficient of the tribe for two genealogical time periods, we computed the combined contribution to the value of F.

In the first stage, the mean \overline{Fxi} for 16 generations is computed by:

$$\overline{Fxi}_{1-16} = (FA_{1-5} + FA_{6-15} + Fxi_{16}) / 16$$

$$\overline{Fxi}_{1-16} = (0.0236 + 0.07468 + 0.004566) / 16 = 0.006427$$

The final F value follows:

$$F = 1 - (1 - \overline{Fxi}_{1-16})^{16} = 0.09802$$

It is note worthy that the obtained value of F is relatively high compared to that recorded in other societies. The F value in the 16th generation, ignoring the contribution of previous generations, will be:

If: $Ne = 846$; $Fx_{15} = 0.00398$; $M = 3\%$;

$$F = [1/2Ne + (2Ne-1)/2Ne \times Fxe] \times (1-M)^2$$

$$F = (0.000591 + 0.999 \times 0.00398) \times 0.041$$

$$F = 0.004297$$

APPENDIX 3:

Child populations compared with our South Sinai Bedouin boys, by place, group, and author(s).

| Country of origin | Designation in graph | Origin of population samples studied | Authors |
|-------------------|----------------------|--------------------------------------|--|
| Egypt | Muzeina | South Sinai | Present study |
| U.S.S.R. | U.S.S.R. | Moscow | Vlastovskii, 1976 |
| France* | France | Paris | Sempe et al., 1971 |
| United Kingdom* | England | London | Tanner et al., 1966 |
| Poland* | Poland-R | Rural | Wolanski, unpubl. |
| Poland | Poland-C | Cracow | Pawel, 1964 |
| U.S.A.* | U.S.A. | Cincinnati | Rauh et al., 1967 |
| U.S.A. | U.S.-W | White | Vital and Health Statistics, 1974 |
| U.S.A. | U.S.-N | Negro | Vital and Health Statistics, 1974 |
| Lebanon* | Lebanon | Various | ICNND, 1962 |
| India* | India A | Well-off | Raghavan et al., 1971 |
| India* | India B | National | Indian Council of Medical Research, 1972 |
| India* | India C | Maharastrians | Sharma, 1970 |
| Israel* | Israel-A | Arabs | Shiloh et al., 1959 |
| Israel | Israel-E.E. | East Europe^ (Jews) | Kobyliansky et al., 1985 |
| Israel | Israel-M.E. | Middle East^ (Jews) | Kobyliansky et al., 1985 |
| Israel | Israel-N.A. | North Africa^ (Jews) | Kobyliansky et al., 1985 |
| Israel | Israel-G | Total (Jews) | Kobyliansky et al., 1985 |
| Senegal* | Senegal | Dakar | Masse, 1969 |
| Mozambique* | Mozambique | Lourenco | Martins, 1968 |
| Tunisia* | Tunisia | Tunis (poor) | H. Boutourline-Young, unpubl. |
| Ethiopia* | Ethiopia | Addis Ababa | Eksmyr, 1971 |
| Egypt* | Egypt-G | National | McDowell et al., 1970 |
| Egypt* | E-1 | Villages | Jasicki, 1965 |
| Egypt | E-2 | Kenouz | El-Nofely, 1978 |
| Egypt | E-3 | Arab | El-Nofely, 1978 |
| Egypt | E-4 | Fededji | El-Nofely, 1978 |
| Egypt | Egypt-Si | Siwah | Pawel, 1964 |
| Egypt | Egypt-Se | Seaside | Pawel, 1964 |
| New Guinea | New Guinea | Kaiapit | Malcolm, 1970 |

* Material taken from Eveleth and Tanner (1976) and consequently these authors are mentioned as a reference point for the source of the material but are not included in the bibliographic list.

^ Origin of parents.

APPENDIX 4:

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