GENETIC HYPOTHESES REQUIRED FOR THE USE OF THE ANIMAL MODEL METHODOLOGY IN HORSE BREEDING

B. LANGLOIS
I.N.R.A. - C.R.J., 78350 JOUY-EN-JOSAS, FRANCE

SUMMARY

The classical approach of the animal model was discussed for a population undergoing selection and homogamy. Reference to a state of equilibrium of the genetic variance was chosen rather than that of the usual base population. A first approach concerning the case where the variance changes was also suggested.

TEXT

The animal model is often considered as an universal solution for the genetic evaluation of horses. HINTZ (1975) was the first scientist who proposed BLUP evaluations and ARNASON (1982) developed the animal model which is now currently used. However, the conditions of application should be more accurately determined so as to evidence some points which require further research.

The genetic hypotheses for the use of animal models are the following :

- the additive heredity of the trait,

- a great number of independent genes governing the trait,

- a genetic correlation between individuals expressed by two-fold the MALECOT'S coefficient of relationship (half the numerator of WRIGHT'S coefficient of relationship).

In these conditions, it was possible to show (KENNEDY and SORENSEN, 1988) that if the heritability value in the base population at panmictic equilibrium was known the model would supply an optimum evaluation of breeding animals and hence of genetic progress due to selection. It is noteworthy that as the evaluations take into account the genetic value of mates, the problem of assortative mating was also considered.

These statements involve :

- knowledge of the heritability of the base population. This is mostly not the case because it is generally the population which is not controlled. Thus, the only available heritability estimates include a more or less large proportion of linkage disequilibrium. However, they are well fitted for evaluation in classical indexation using regression as suggested by LANGLOIS (1988a,b). But on account of present developments this procedure is however archaic.

- the stability of the genic variance σ^2A defined as the genetic variance achieved in panmixia with the same genic frequencies. This constancy determines that of the variance of errors due to meïotic sampling. The expression of this intra family variance is indeed very important. According

to BULMER (1980) it is assumed that $Var(e) = \sigma^2 A (1-F)/2$, but this is only true in certain condition in particular the stability of genic variances in the parents and the absence of linkage disequilibrium. We supplied a more general expression (LANGLOIS, 1990). However, when using the animal model the main point is not the expression of this variance but rather its stability which cannot always be obtained immediately.

- the expression of the covariance between relatives as two-fold MALECOT'S coefficient of relationship multiplied by the genic variance. However, this is true in the case of selection while it is not true when the population undergoes homogamy (FISHER 1918, WRIGHT 1921, LATTER, 1965, CROW and KIMURA, 1970, BULMER, 1980, GIMELFARB, 1981 a and b, LANGLOIS, 1975 and 1981, NAGYLAKI, 1978 and TALLIS, 1985).

At the present time, we attempt to generalize the expression of covariance beetween relatives different from that proposed by COCHERHAM (1954) or KEMPTHORNE (1957). The approach is the following :

According to the genetic model :

$$A_i = (A_s + A_d)/2 + e \tag{1}$$

where A represents the additive genetic value, i, s and d indicating the animal, its sire and dam, respectively.

where e represents the prediction error due to meiosis aleas, e is independent of A_s et A_d.

We have then :

$$Cov(A_i, A_s) = Var(A_s)/2 + Cov(A_s, A_d)/2 \tag{2}$$

$$Cov(A_i, A_d) = Var(A_d)/2 + Cov(A_s, A_d)/2 \tag{3}$$

In addition, we have :

$$Cov(A_i, A_j) = Cov(A_i, A_s) \, Cov(A_s, A_j)/Var(A_s)$$
$$+ Cov(A_i, A_d) \, Cov(A_d, A_j)/Var(A_d) \tag{4}$$

which, with (2) and (3), leads to :

$$Cov(A_i, A_j) = Cov(A_s, A_j) \, [1 + b^{\wedge d}/A_s]/2$$
$$+ Cov(A_d, A_j) \, [1 + b^{\wedge s}/A_d]/2 \tag{5}$$

where b is the regression coefficient of A_d on A_s or of A_s on A_d.

Moreover :

$$Var(A_i) = [Var(A_s) + Var(A_d)]/4 + Cov(A_s, A_d)/2$$
$$+ Var(e) \tag{6}$$

if dividing the equations (5) and (6) by :

$$Var(A_i) - Cov(A_s, A_d)/2 = [var(A_s) + Var(A_d)]/4 + Var(e)$$

we can define coefficients b_{ij}, b_{m7}, b_{dj}, b_{ii} and b_{md} such as :

$$\left\{ \begin{array}{ll} b_{ij} = (1 + b^{nd}/_{nm}) \, b_{mj}/2 + (1 + b^{nm}/_{nd})b_{dj}/2 & (7) \\ \\ b_{ji} = 1 + b_{md}/2 & (8) \end{array} \right.$$

This system of recurrent equations differ markedly from that usually proposed to calculate two-fold MALECOT'S coefficients of relationship, ϕij

$$\left\{ \begin{array}{lll} a_{ij} = a_{mj}/2 + a_{dj}/2 & \text{for } i > j & (9) \\ \\ a_{ii} = 1 + a_{md}/2 & \text{for } i = j & (10) \end{array} \right.$$

Then if $a_{jj} = 2 \, \phi_{ij}$, b_{ij} is only equal to the former if $\text{Cov}(A_m, A_d) = 0$. In the other cases b_{ij} is very different from a_{ij}. However, apart from one corrective factor it also expresses the relationships between additive genetic values.

It can be shown for all i and j according to their definitions that :

$$\text{Cov } (A_j, A_j) = b_{ij} \quad [\text{Var}(A_i) - \text{Cov}(A_m, A_d)/2]$$

It should also be noticed that bij is calculated in the same way as $2 \, \phi ij$, but that whenever we use 1/2 in the path beetween two generations, we use $1/2 \, (1 + b^{nd}/_{nm})$ in the path from sire to offspring and $1/2 \, (1 + b^{nm}/_{nd})$ in the path from dam to offspring. Assuming that $\text{Cov}(A_m, A_d)$ is constant for any generation and $\text{Var}(A_m) = \text{Var}(A_d)$ led FISHER (1918) to express the correlation grandparent-offspring, great-grandparent offspring etc. The general case is more complicated because selection leads often to dissymetric paternal and maternal path and because it is also difficult to assume the constance of genetic variance and hence that of the covariance between mates.

On the basis of this observations it appears that the animal model in its usual approach underestimates the correlations between genetic value of animals when $\text{Cov } (A_m, A_d) \neq 0$. However, in many cases this does not seem to be a big problem.

However, the approach could also be used when the genetic correlation between mates is different from zero. The easiest way of doing would then be to assume that the correlation is constant providing the existence of a stable genetic variance.

Instead of the hypothesis on the base population we would then use a genetic equilibrium for all animals studied whatever their generation or year of birth.

In the other cases genetic parameters varying according to generation or year of birth should be available. These parameters can be estimated using subsamples of the file and this makes our approach different from the classical one.

REFERENCES

ARNASON, T. 1982. EAAP, Horse commission, Leningrad, 16-19 Août, H1.1.1

BULMER, M.G. 1980. Clarendon, Press, Oxford 254 p.

COCHERHAM, 1954. Genetics, 39, 859.

CROW, J.F., KIMURA, M. 1970. Harper et Row, New York, 591 p.

FISHER, R.A. 1918. Trans. Roy. Soc. Edimb., 52, 399-433.

GIMELFARB, A. 1981a. J. Math. Biology, 13, 209-226.

GIMELFARB, A. 1981b. J. Math. Biology, 13, 227-240.

KEMPTHORNE, O. 1957. John Wiley and Sons, New York, 545 p.

KENNEDY, B.W., SORENSEN, D.A. 1988. Proc. Int. Conf. Quant. Genet. ch. 9, 91-101.

LANGLOIS, B. 1975. Ann. Génét. Sél. anim., 7, 387-408.

LANGLOIS, B. 1981. ann. Génét. Sél. anim., 13, 151-164.

LANGLOIS, B. 1988a. Proc. V. Intern. Symp. Horse breeding. Leipzig, Vol 1, 237-257.

LANGLOIS, B. 1988b. EAAP Publication n° 42, 27-40, Pudoc Wageningen.

LANGLOIS, B. 1990. G.S.E., 22, (1) in press.

LATTER, B.D.H. 1965. Genet. Res., 6, 360-370.

MALECOT, G. 1948. Masson, Paris.

NAGYLAKI, T. 1978. Ann. Hum. Genet., 42, 131-137.

TALLIS, G.M. 1985. T.A.G., 70, 497-504.

VAN VLECK, L.D., HINTZ, R.L. 1975. Proc. of Int. Symp. on genet. and horse breeding Royal Dublin Society. 19-23.

WRIGHT, S. 1921. Genetics, 6, 144-161.