

NEED AND METHODS OF GENE CONSERVATION IN ANIMAL BREEDING (*)

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SUMMARY

The problem of gene losses was considered topical at least in cattle and poultry, possibly also in pigs and sheep. The need of preventing them is determined by several factors: 1) Past experience of actual losses; 2) probable effect of present breeding methods on the genetic variability (both selection and random drift); 3) changing demand for animal products because of new knowledge in food science, rising living standard, new fashions, increased quality requirement, need of lower production costs, need of bigger quantities, etc.; 4) changes in environment (feeding, housing, managements, disease); 5) experiences from plant breeding; 6) existence of unexamined breeds; 7) better utilization of land; 8) utilization of hybrid vigor; 9) difficulties in creating new useful variation.

The available methods of gene conservation were discussed, the main attention being paid to the maintenance of small nuclei of most breeds and strains, to the establishment of gene pools, and to the establishment of frozen semen banks. Finally, organisation and principles of gene pools were briefly discussed, and the need of a coordinating international body was indicated.

I. — INTRODUCTION

The present era of frozen semen in cattle A.I. has re-actualized the problem of gene losses, which was amply discussed a few decades ago when the A.I. breeding was at the stage of a final breakthrough (EDWARDS, 1959). The second species in which this problem has become topical is the poultry, where the exceptional reproductive rate makes it possible to disseminate selected material very rapidly, thus concentrating the actual breeding work into the hands of very few enterprisers. Without doubt the problem is of some importance even in pigs and sheep, and it may be well-founded to consider almost the entire animal kingdom, in order that no species which might be of value to mankind in the future, would unnecessarily be lost.

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The problem arises mainly from the fact that an effective utilization of the best animals of to-day automatically means setting aside the poorer animals, strains, breeds, and even species. The purpose of the present paper is to consider, (1) whether this elimination of genetic material will have undesirable consequences, and (2) if so, how these could be avoided.

II. — THE NEED OF GENE CONSERVATION

The need of adopting special measures for preventing loss of genes is determined by several groups of factors, e. g. the occurrence of actual gene losses in the past, the probable effect of present breeding systems on the genetic variability, the possible changes in the demand of various human foods, and possible future changes in the environmental conditions of farm animals.

A. — *Losses or nearby losses of breeds and strains*

Before the beginning of rational animal breeding, i. e. 50-100 years ago, there were numerous local native *breeds* of different species, obviously well adapted to the primitive conditions of that time. Many of these breeds have been replaced by other breeds, which were considered superior to them. It is difficult to avoid the impression that the choice of breeds was often based on rather superficial knowledge, biased by many environmental factors, since even now objective knowledge of the merits of different breeds is scarce. The importance given to the purity of breeds favoured the complete discarding of breeds with slightly inferior total merits, and hence any genes of special merit were lost together with the breeds discarded. Later on, many internationally well known breeds have undergone the same fate. The use of up-grading has meant a little more cautious treatment of the gene pools of the inferior stocks, but not very decisively so, except in cases where cross-bred males have been accepted for extensive use. In a random sample of 50 registered Finnish Ayrshire cows born in 1955 the proportion of imported genes was 95 p. 100.

It would be interesting to prepare a list of breeds having disappeared during the last 100 years, but since this would go far beyond the time and energy available for me, I shall confine myself to mention some examples from my nearest vicinity. In Finland, the *North-Finnish* type of native cattle (*Finncattle*) has almost entirely disappeared, the frequency of the *East-Finnish* type has considerably decreased, and even the *West-Finnish* type is losing ground to the bigger-sized *Ayrshire* and *Friesian* breeds, although it is not yet settled whether one should strive for bigger animals for the sake of beef production. Fortunately, some genes of the different types of *Finncattle* will be saved, thanks to the moderately liberal breeding policy of the respective breed society.

An idea of the importance of a cautious displacement is given by fig. 1, which shows that hardly 30 p. 100 of the alleles of the B blood group system occurring in *West-Finnish* and *Ayrshire* bulls were common to both groups of bulls, while about 18 p. 100 of the alleles occurred only in *Ayrshire* and 50 p. 100 only in the

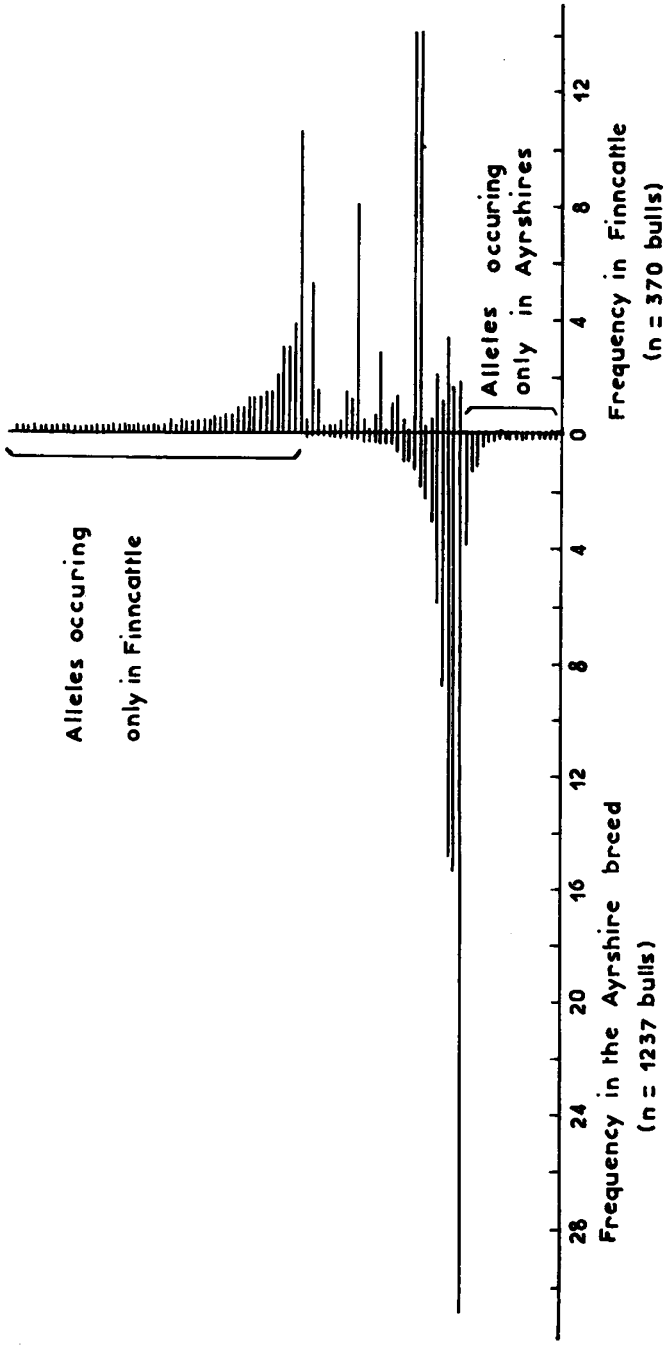


FIG. 1. — Frequencies of different alleles of the B blood group system in *Ayrshire* and *Finnccattle* breed according to the study by MAIJALA and LINDSTROM (1966).

FIG. 1. — *Frequences des differents alleles du systeme de groupe sanguin B dans les races bovines Ayrshire et Finnnoise (d'après MAIJALA et LINDSTROM, 1966).*

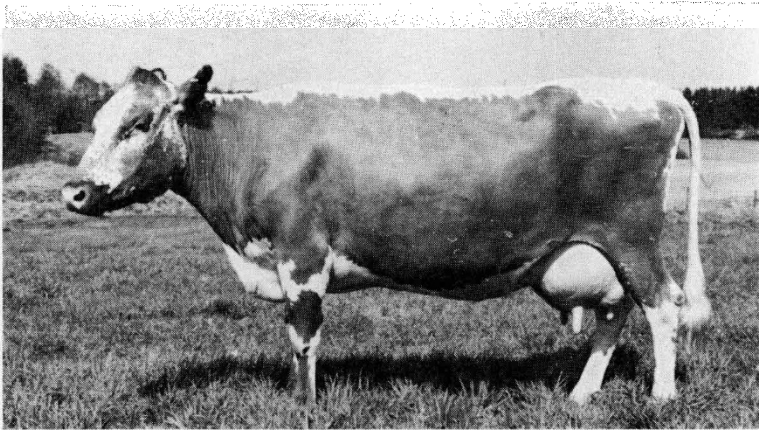
West-Finnish cattle. In case this dissimilarity of blood group alleles partly reflects differences in the genetic make-up affecting production traits, a total loss of the *Finncattle* genes would obviously mean a serious decay of genetic variability of cattle in Finland. The difference in milk yield between the two breeds is nearly 20 p. 100, but partly this difference can be explained by the difference of nearly 10 p. 100 in the adult live weight. In the growth rate of performance tested young bulls up to 6 months, there were almost no difference (LINDSTROM and MAIJALA, 1969). Thus it is possible that even a given quantitative trait may partly be determined by different sets of genes in two breeds. The average non-return rate of *Finncattle* is 3-4 p. 100 higher than that of Ayrshire. Another special advantage of the *Finncattle* is its polledness (fig. 2).

Recently the *Finnish Landrace* sheep (*Finnsheep*) (fig. 3) was also approaching extinction, as the population decreased from over 1 mill. head in 1950 to 0.15 mill. in 1967, and sheep breeds with better muscling and growth rate were simultaneously being looked for. Recently it has been realized, however, that the fertility genes of *Finnsheep* might be useful in intensive production of lamb meat. A third Finnish example is the native hen, the good brooding instinct of which was no longer required when the artificial incubators became popular. It may have possessed also other capabilities, like resistance to some diseases, longevity and unpretentiousness, but these were not properly investigated before the breed was lost.

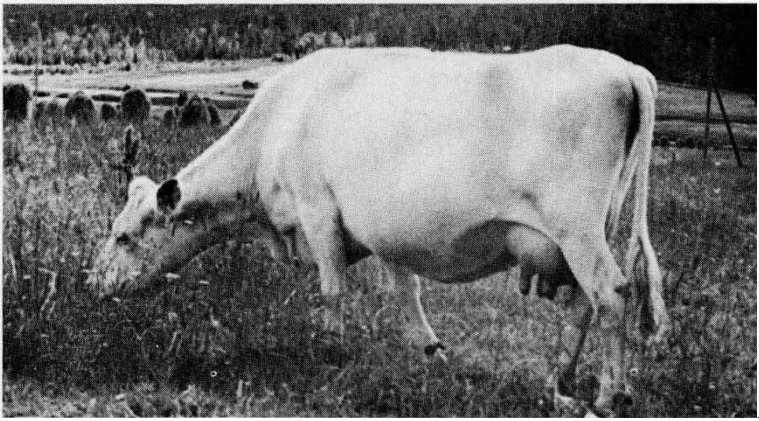
In Sweden, the situation with regard to the *Swedish Polled Cattle* is very similar to that of *Finncattle*. In Norway, there were about 30 breeds of cattle in the 1930's, but now hardly every tenth is left. A part of the genes of the vanished breeds has been saved by the liberal use of crossbred bulls in A.I.. At least half of the British cattle breeds listed by HOUSMAN (1905) are approaching extinction (MMB, 1968). According to BOYER (1964) there are 19 local breeds of hens in France near extinction, and VAN ALBADA (1964) reports about a similar number for the Netherlands. In general, the so-called "half-heavy poultry breeds" started to disappear after the specialization into broiler and egg-type breeds became popular.

Of course, even a long list of breeds which have disappeared, does not mean much in case one could be sure that they didn't possess genes which could be useful in future animal breeding. The recent «discoveries» of the leukosis-resistant *Fayoumi-hen* from Egypt, the muscular *Cornish* game-cock from India, and the fast-growing *Charolais* cattle from France, as well as of some fertile or muscular sheep breeds form examples that changes in the environment or in the market may bring to light the usefulness of breeds which were previously considered to be of little commercial value. Even the recent creation of useful compound breeds as *Beltsville n° 1*, *Minnesota n° 1* and *n° 2*, *Lacombe*, *Santa Gertrudis* etc. speak in favour of preserving breeds from extinction.

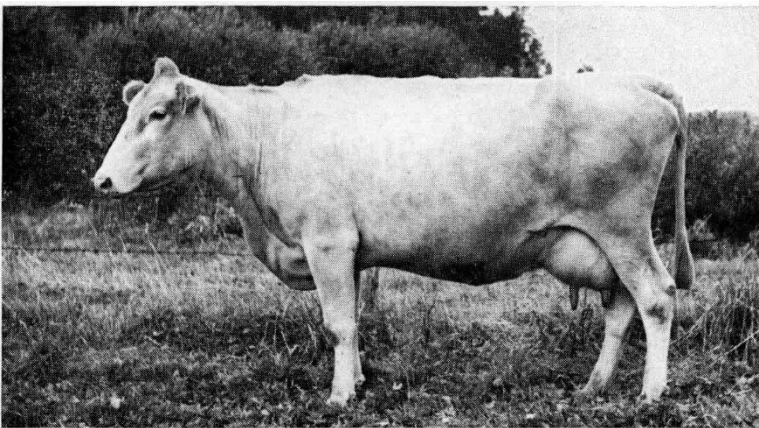
In poultry breeding, there has been some decrease in the number of *strains* within breeds in the last two decades, because of the decrease in the number of breeders. According to VAN ALBADA (1964) and OROZCO (1964) the number of strains has not decreased as rapidly as that of breeders, as the remaining breeders have increased the numbers of their lines at the same time. It is probable, howe-



(a)



(b)



(c)

FIG. 2. — The three types within the native Finnish cattle breed (*Finncattle*). The east (a) and northern (b) types are rapidly losing in strength and will probably soon be more or less entirely replaced by the western type (c), which in turn is losing grounds to *Ayrshire* and *Friesian* cattle.

FIG. 2. — Les trois types constituant la race bovine finnoise indigène (*Finncattle*). En diminution rapide, les deux types orientaux (a) et nordique (b) vont sans doute bientôt être remplacés plus ou moins totalement par le type occidental (c) lui-même en recul devant les races *Ayrshire* et *Frisonne*.



FIG. 3. — The *Finnish Landrace* sheep (*Finnsheep*) is an exceptionally prolific breed, the population of which was rapidly decreasing in numbers during the last two decades.

FIG. 3. — *Le mouton finnois Landrace* (*Finnsheep*) est une race exceptionnellement prolifique. Durant les deux dernières décades l'effectif racial s'est cependant rapidement réduit.

ver, that the new strains in many cases are sub-strains of the previous strains of the surviving breeders, and not based on the strains of the unlucky competitors. Some American poultry breeders have claimed that it is difficult to find new strains which could successfully be used for further improvement of their hens, while JAAP (1966) made the interesting observation that alleles carried by slow-growing egg-production strains may have value for improving the growth rate of broilers. This is apt to support the hypothesis that a given quantitative trait may be determined by different genes in different populations, and that combining two or several such strains would give a good basis for selection. On the other hand, LERNER and DONALD (1966) consider that the two extreme breeds, *Friesian* and *Jersey*, might well include all the genes needed in the future cattle breeding. In any case, it is reasonable to think that a loss of a strain with exceptional gene material is more detrimental than a loss of a strain having an exceptional frequency of the genes occurring in the remaining strains (OROZCO, 1964). It is also clear that the establishment of Random Sample Tests and other improvements in testing methods, as well as the introduction of more and more efficient propagation methods, are inclined to increase the risk of losing interesting strains.

B. — *Effect of breed improvement on the genetic variability*

Although the losses of genes caused by culling entire breeds or strains obviously are the most serious ones, it is necessary to consider also the within-population losses caused by selection and chance.

1. *Decay of variability due to selection*

A natural consequence of successful efforts to increase the frequency of "good" genes and to decrease that of "bad" genes is a decay of genetic variability, although the experiences obtained in this respect are conflicting. In many cases it has been difficult to notice much of decrease in the phenotypic variability, in spite of considerable changes in the mean performance (e.g. FALCONER, 1955). On the other hand, many workers with laboratory animals or poultry have experienced a "ceiling" or "plateau" in their selection attempts, within a number of generations, and this lack of response has sometimes come rather abruptly, without obvious signs of warning (FALCONER, 1955, CLAYTON and ROBERTSON, 1957). However, negative genetic correlations between the trait selected for and fitness traits, or a continuously varying environment, have been considered as main causes rather than any decay in genetic variability (DICKERSON 1955, ROBERTSON 1955). LERNER and DONALD (1966) considered that ,, gains in selection are always achieved at the cost of reducing variance ", and that ,, sooner or later genetic variability which responds to a certain system will approach exhaustion ".

In addition to selection experiments with laboratory animals, some simulation studies have given valuable information of the probable effects of selection. For example, YOUNG (1966), working with an imagined population of 1.000 individuals, considered 3 levels of selection intensity, 3 levels of initial heritability, 3 levels of recombination probability and 7 genetic models. It was assumed that the trait was controlled by 10 loci, and that the initial gene frequency at each locus was 0.5. The additive model led to the changes of additive variance shown in fig. 4 in YOUNG's paper. It appears that the decay of variance can be very rapid, if one selects strongly for a trait with a high heritability. Even a medium heritability of 0.4 led to a total loss of additive variance within 14 generations, when only 10 p. 100 of the individuals were selected. Considering all the genetic models tried, the full-lives of additive variance under the same conditions varied from 9 to over 30 generations, and the half-lives between 1.4 and 4.3 generations. In the former case the dominance model gave the highest value, while in the latter case it showed the lowest. The importance of linkage in determining the rate of decay was comparatively small. As a whole, it appears that the losses of genes caused by directional selection may often be worth considering when plans for additional improvement of animals are being made.

2. *Gene losses due to random drift.*

In small populations, one can lose genes even by chance, due to the random fluctuation of gene frequency, and these losses can be enhanced by intentional mating of related individuals. These losses are undirectional, since they affect the favourable and unfavourable genes with equal probability. In the populations analyzed so far the average decrease of heterozygosity has been a good 0.5 % per generation (LUSH, 1947), and it has been difficult to show that A.I. would have increased the figure in cattle populations (ROTTENSTEN, 1961). Because of the intentional avoidance of inbreeding in A.I. operations, the actual

coefficient of inbreeding is not very suitable for measuring gene losses, but these should be measured by the expected inbreeding coefficient, based on the average coefficient of relationship (RENDEL, 1958 and 1963, MAIJALA and LINDSTROM 1966). In the studies reviewed by RENDEL (1967) the expected homozygosity of B blood group alleles varied between 4.0 and 24.8 %, and the number of different B-alleles in different breeds from 20 to 132.

Future gene losses due to random drift can be predicted with the aid of the concept of effective population size (N_e) introduced by WRIGHT (1931). Considering that the loss of heterozygosity per generation is approximately proportional

to $\frac{1}{2 N_e}$ the critical values of N_e lie between 50 and 10:

Effective population size, N_e	50	40	30	20	10
Loss of heterozyg./generat., %	1.00	1.25	1.67	2.50	5.00
No. of sires/gener. (cattle)	12.5	10.0	7.5	5.0	2.5

It has now become possible to approach these values in Finland and many other countries where frozen semen is used exclusively. One half of the 200 young *Ayrshire* bulls on the performance testing station are sons of one bull, which still is fully active and from which over 50 000 pellets already have been stored.

According to a recent simulation study (EBBERSTEN et al. 1969) the average number of generations required for fixing a gene with an initial frequency of 0.5 was as follows:

Population size :	5	10	15	20	25	30
No. of generations	15	23	37	47	72	125

A comparison of these figures with the full-lives of additive variance obtained by YOUNG (1966) reveals that the decay of variability caused by random drift is somewhat slower than that caused by directional selection, thus supporting the results obtained by ROBERTSON (1960).

C. — Changing demand for animal products

In the past there have been so many changes in the demand for various products on the market of different countries, that it may not be difficult to agree as to the necessity of maintaining a reasonable amount of variability in our animal populations, in order to be able to cope with future changes. The changes may be caused by one or several of the following factors :

1. New knowledge in the field of human nutrition, enhancing the value of some nutrients or dooming some products as unwholesome.
2. Increasing standard of living, making possible an increased consumption of nutritionally valuable but expensive foods (e.g. meat) or of foods with special taste (game animals).

3. New fashions in clothing (furs) or eating (brown eggs).
4. Increased quality requirements with regard to conventional products (leaner meat, protein-rich milk, strong eggshells etc.).
5. Necessity to decrease the costs of production (feed conversion, ease-of-milking, calm temper), in order to be able to compete with industrial products or substitutes.
6. Increased requirements with regard to quantity, in order to combat hunger (reproduction ability, growth capacity).
7. Necessity to compensate the exhaustion of natural reserves of some materials (fuels, minerals).
8. Necessity of finding new ways of utilizing agricultural plant products in case of surplus problems.

D. — *Changes in the environmental conditions of farm animals*

The need of breeding different kinds of animals for different environments depends on the existence and magnitude of non-linear interaction between heredity and environment. Although the experimental results bearing upon this problem have been rather conflicting, more and more positive evidence has been accumulating during recent years, especially in poultry (MERAT, 1968). The interaction seems to concern particularly mortality and egg production. In a study by NORDSKOG and KEMPTHORNE (1960) the strain \times farm interaction accounted for no less than 31 p. 100 of the total variance among pen means for mortality, and the genetic correlation between mortality figures of the same production stock kept in different locations was only 0.03. It is obvious that the importance of these interactions will vary with the species, character and the diversity of environment. Taking into account that some of the studies showing no genotype-environment interaction were based on slightly varying or poorly defined environments, and that specialization of environments is a likely direction of development, it appears well-founded to maintain enough variability for fitting animals for special environments. This may in some cases be cheaper than to fit the environment for special animals. The possible changes of environment can be grouped as follows :

1. Changes in feeding. New economic feeds can be found, which may be inadequate in some respect (lack of concentration, certain essential amino acids, fatty acids, minerals or other qualities). It has been shown that there are some variations between breeds, strains and individuals in the utilization of nutrients (NESHEIM, 1966).

2. New diseases may occur. It is true that in most cases effective medicines can be devised and produced much faster than resistant lines of animals, especially in large animals with slow reproductive rate. However, it has proved difficult to find medicines against viruses.

3. Developments in housing (regulation of temperature, moisture etc.) may make it possible to utilize specialized animals, which are not able to compete in

conventional conditions. Lack of proper housing facilities also requires, perhaps, special animals.

4. Changes in management may increase the desirability of certain traits (suitability for machine milking, polled animals for loose housing, certain colour genes for autosexing, out-of-season lambing for intensive lamb meat production, special battery hens).

E. — *Miscellaneous aspects*

Several other aspects bearing upon the importance of conserving genes appear from the reports of some meetings discussing the problem (HODGSON, 1961, SCOSSIROLI 1964, VAN ALBADA 1964, SHS 1965, MENZI 1966, FAO 1966). These include also discussions on experiences obtained in plant breeding, the existence of numerous unexamined breeds in the developing countries, the need of improving the utilization of land, and the possibility of utilizing hybrid vigor.

III. — METHODS OF GENE CONSERVATION

Although the aspects speaking in favour of gene conservation may have received too much attention above, at the expense of opposite arguments, it is obviously valuable to search for and apply some cheap and efficient methods for preventing unnecessary or serious losses of genes. There are at least three different methods to be considered seriously:

- (1) maintenance of several pure breeds or strains,
- (2) establishment of a common gene pool, and
- (3) establishment of banks for frozen semen, eggs or gonadal tissues.

A fourth possibility open to groups of breeders would be bringing in genes from other breeds or countries, but this presupposes that somebody else has taken care of the conservation. A cautious selection would be a fifth alternative, but the slow progress resulting from it on thousands of farms makes it a very expensive method.

The choice between the two first-mentioned methods obviously depends on the size and reproductive ability of the species, as the maintenance of large animals in numbers big enough to avoid random losses of genes is expensive, unless the particular breed has a good average performance. It may be necessary to apply both methods in most species, but relatively fewer breeds can be kept pure in large livestock species than in the small ones. Another factor determining the choice consists of the kind of traits each breed possesses, and of the purposes of its preservation. Breeds which have some special traits well developed, deserve to be kept as « pure elements on the shelves of the chemist », while an amalgamation into a gene pool may be an appropriate method for a breed whose average performance is assumed to be caused by exceptional sets of genes. This is also the most likely method to be used for a breed, the value of which is not known. Preservation of valuable strains as independent populations is particularly important for the utilization of non-additive inheritance. In any case, there is a question of preserving genes rather than breeds.

In cattle, maintenance of many breeds or of a gene pool can now be managed in the form of frozen semen. It is not yet completely known how long the frozen semen maintains its fertilizing capacity in liquid nitrogen, and hence one cannot yet base long-term plans upon frozen semen. However, it would be important to save some doses of semen from every breed or strain which is likely to become extinct within the next few years. As far as is known to me, freezing of eggs or gonadal tissues is not yet of practical value in this respect.

The costs of maintaining pure breeds or gene pools could, perhaps, be decreased by combining the activities with those of zoological gardens or with other leisure time businesses. This might be a fertile field for international cooperation between nature-conserving zoologists and animal geneticists. It may also pay to encourage and subsidize so-called fancy breeders to keep animals of rare breeds.

There is a wide range of opinions among animal geneticists: some workers don't consider it worthwhile to worry about the conservation of genes, while

others don't dare to utilize the present possibilities for selection, in order not to endanger future possibilities. The former attitude is sometimes based on the belief that useful genetic variation can be created with the aid of mutagens whenever required, while the advocates of the latter view consider that most of the mutations to be brought about would be undesirable, and that the testing of their usefulness would take too long time. The truth probably lies somewhere between the two extreme opinions, but where? According to the experiments performed so far, the importance of induced mutations for short-term progress in quantitative traits has been very small, but the frequency of lethals has increased considerably (ROBERTSON, 1955 *b*). LERNER and DONALD (1966) consider that the abundance of undesirable mutations makes the creation of new variability too expensive. The same authors thought that every generation has a duty to look after the maintenance of genetic variation, but that economic reasons often tempt one to act against this duty. However, the slowness of developmental processes and the obstinacy of many individual breeders are of great help in fulfilling the duty, at least for the present.

IV. — ORGANISATION AND PRINCIPLES OF GENE POOLS

The principles to be applied in establishing and maintaining gene pools have been discussed by JAAP (1964), BOYER (1964), OROZCO (1964) and FAO (1966). The basic step is to make an inventory of all available stocks, including collected informations of the characteristics of each stock. Then the most useful or interesting stocks are tried in a common environment, after which the final choice of strains to be conserved is made. According to JAAP it is inadvisable to combine more than 2-3 populations into a pool, in order to keep the frequencies of most alleles at a useful level. This determines the number of populations to be maintained. He recommended 40 pairs of parents per generation and at least 10 offspring from each pair for each population. Matings should be randomized and the effects of natural selection should be avoided. One central station is usually recommended, but in cases where each strain has been kept pure, some private farms have been utilized.

From the global or continental point of view, it might be well-founded to encourage each country to take care of the preservation of its own national breeds and to keep the coordinating international body, e.g. FAO, well informed of the numbers and characteristics of the stocks. In case there is temptation to destroy a breed, it would be advisable to negotiate first with the coordinating body, which for this purpose should have a responsible official and an advisory council. In evaluating national stocks, some widely distributed international breeds could be used as controls.

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RÉSUMÉ

COMMENT SAUVEGARDER LA VARIABILITÉ GÉNÉTIQUE NÉCESSAIRE A L'ÉLEVAGE

Dès maintenant, le problème de la perte des gènes se pose avec acuité chez les bovins et la Poule, peut-être aussi chez le Porc et le Mouton. L'expérience des pertes passées et l'effet probable des méthodes actuelles d'élevage sur la variabilité génétique (à la fois sélection et dérive aléatoire) nous incitent fortement à lutter contre cette tendance. Il est aussi d'autres raisons qui plaident en faveur de la conservation de la diversité génique : l'évolution de la demande en produits animaux résultant des nouvelles connaissances en diététique, de l'augmentation du niveau de vie, des nouvelles modes, des exigences qualitatives accrues, de besoin d'abaisser les coûts de production et d'augmenter les rendements; les changements dans l'environnement (alimentation, logement, élevage, maladies...); l'expérience de la culture des plantes; l'existence de races non encore inventoriées génétiquement; une meilleure utilisation du sol; l'emploi de la vigueur hybride et, enfin, la difficulté de créer de nouvelles variations utiles.

Parmi les différentes méthodes de conservation des gènes on a surtout envisagé le maintien de petits noyaux de la plupart des races et lignées, l'établissement de lignées polyalléliques et la création de banques de sperme. Pour finir, le principe et la mise en place des lignées polyalléliques sont brièvement analysés. La création d'un organisme international pour la coordination des efforts semble nécessaire.

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