
THE PROCEEDINGS OF THE
NEW ZEALAND SOCIETY
OF
ANIMAL PRODUCTION
VOLUME 62 2002

GENETIC IMPROVEMENT OF DAIRY CATTLE

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SUMMARY

The effect of selection depends on (1) the accuracy in the estimation of the breeding value of individual animals, (2) the selection differential, (3) the genetic variation in the population, and (4) the length of the generation interval. The first and second of these factors can be increased by the breeder and the fourth can be decreased, thus increasing the selection response per unit of time. The most powerful tools in dairy breed improvement are an efficient bull progeny testing of a fairly large number of bulls and an intensive selection among the tested bulls. The organization of A.I. breeding in Norway is briefly described. At present it is probably the most efficient scheme for dairy cattle improvement which has been initiated anywhere.

CONSIDERATION of this topic will be limited to the improvement of quantitative traits which directly or indirectly influence the economy of milk production. In general, it may be said that the variation of such traits in a certain population depends on genetic differences between the individuals, the environmental variations, and the interaction between genotypes and the environment. The genetic variation is, as a rule, due to a large number of genes which individually have minor effects (polygenes). It is not feasible to show in detail how such traits are inherited, but, by the use of statistical methods in the treatment of suitable data, it is possible to estimate how large parts of the total variation within the population may be attributed to genetic and to environmental factors, that is, the heritability of the trait in question. It may also be possible to estimate the part due to genotype-environment interactions. The term heritability is here used in "the narrow sense" — *i.e.*, heritability depending on the additive (or average) effect of the genes in their various combinations. For a rational planning of the breeding procedures, the variation, usually measured in standard deviation units, and the heritability of the traits which will be subjected to selection, need to be known. It is also valuable to know something about the genetic and environmental correlation between the various traits. Table 1

TABLE 1: HERITABILITY (h^2) AND STANDARD DEVIATION (s) OF DAIRY CATTLE TRAITS. MAINLY BASED ON EUROPEAN INVESTIGATIONS.

Trait	*Heritability*	*Standard Deviation*
Body size at maturity:		
Weight (kg)	0.40	40-50
Height at withers (cm)	0.50	3.5
Milk yield (305 d, 1st lactation) (kg)	0.30	700-900
Milk composition:		
Fat content (%)	0.60	0.30
Protein content (%)	0.50	0.19
Solids-not-fat content (%)	0.55	0.23
Ease of milking: average flow (kg/min) (corrected for yield)	0.70	0.50
Udder proportions: front quarters in % of total yield:		
Friesian and Red Danish	0.50	5-6
Danish Jersey	0.30	6
Measures of female fertility:		
Calving interval (days)	< 0.05	65-75
Non return rate (days)	< 0.05	—
Length of pregnancy:		
Depending on genotype of foetus (days)	0.30	5
Repeatability (within cows)	0.15	—

shows approximate values for the two parameters heritability and standard deviation of some important traits of dairy cattle, when estimated for large breeding populations, for example, a breed within a certain area.

All data for milk yield and composition, as well as ease of milking, refer to the first lactation. The milk records are not corrected to yield at maturity. These two facts probably explain why the estimate for heritability of milk yield is somewhat higher than according to American investigations.

The heritabilities of calving interval and non-return rate are low but it must be remembered that both are very crude measures of female fertility. Analysis of breeding records of A.I. bulls have shown rather high repeatabilities between years of their non-return rates (0.4 to 0.6). Some types of gamete sterility and genital malformation show simple Mendelian inheritance.

In Table 2, figures are presented indicating the phenotypic and genetic correlations between some of the traits which are listed in Table 1. Numerous studies have been made on the correlation between body size and milk yield but the results are conflicting and difficult to interpret

TABLE 2: PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN TRAITS (FRIESIAN CATTLE)

	Phenotypic (r_p)	*Genetic* (r_g)
Body size and type (mature cows):		
Weight (after calving) — milk yield	(0.1-0.2)	(0.2)
Height at withers — milk yield	(0.2-0.3)	(0.3)
"Beef type" (score) — milk yield	(0.1-0.2)†	—(0.44)†
Milk yield — butterfat (and protein) (%)	—0.2	—0.35
Butterfat % — protein %	0.55	0.65
Butterfat % — solids-not-fat %	0.5	0.6

†According to Dutch investigation (Bosma, 1961; Bekedam, 1964).

owing to various sources of systematical errors. However, there are good agreements showing a higher correlation between withers height and yield than between body weight and yield. Dutch investigations point rather definitely to negative correlations between the degree of "dual-purpose type" of Friesian cattle and milk yield. Some investigations indicate that the negative correlation between milk yield and fat content is more pronounced in breeds which produce milk high in fat — *e.g.*, Jersey and Guernsey — than for breeds with milk low in fat — *e.g.*, Friesians. The phenotypic and genetic correlations between the fat content and protein content of the milk are found to be rather high.

THE EFFECT OF SELECTION

Selective breeding is the most powerful tool in breed improvement. The effect of selection per unit of time depends on the following four factors:

(1) The accuracy of estimation of the breeding value (or genotype) of animals considered for breeding. This accuracy is measured by the correlation (r_{AI}) between the breeding value of the animal (A) and the index (I) on which the selection is based. The squared correlation equals the heritability of the index: $r_{AI}^2 = h_I^2$. The index may be the animal's own performance or a combination of information from several sources.

(2) The selection differential (S), defined as the difference between the animals chosen for breeding and the average of the whole generation to which they belong. The selection differential (Fig. 1) is usually expressed in

standard deviation units ($S/s = i$). Selection intensity is defined as the proportion of the animals produced in a given generation which are selected for breeding. This proportion (v) can be calculated from tables of ordinates and area of the normal curve: $i = z/v$ where z is the height of the ordinate which separates v from ($1-v$).

(3) The genetic variation in the whole generation of animals among which we select, measured by the standard deviation of the true breeding values (σ_A). This variation can be estimated as the product of the square root of h_I^2 and the phenotypic standard variation (s_p), or $r_{AI} \cdot s_p$.

(4) The generation interval (y), defined as the average time interval between the birth of parents and their progeny which are used for breeding. For dairy cattle this interval is on an average 5 to 6 years.

TABLE 3: ESTIMATED SELECTION EFFECT AND THE RELATIVE CONTRIBUTION OF PARENTS TO THE GENETIC GAIN UNDER SPECIFIED CONDITIONS. A.I. BREEDING.

I. *Optimum breeding structure under A.I. and selection for milk yield only.*	*Size of the milk recorded cow population*		
	2,000	*20,000*	*400,000*
(Skjervold, 1967; Lindstrom, 1968)	*cows*	*cows*	*cows*
Possible yield improvement per year	1.7%	2.5%	3.4%
Relative contribution of parents to genetic gain of offspring:			
Sires (progeny tested) ⟶ Sons	43%	50%	62%
Sires (50% tested) ⟶ Daughters	18%	21%	15%
Dams ⟶ Sons	33%	23%	18%
Dams ⟶ Daughters	6%	6%	5%
II. *Example of achievement in practice: Slack selection on progeny test. Several traits considered.*	*Norwegian Red cattle (Syrstad, 1966)*		*Finnish Ayrshire (Lindstrom, 1968)*
	1957-61	*1962-4*	*1961-6*
Estimated improvement per year	0.8%	1.0%	0.8%
Relative contribution of parents to genetic gain of offspring:			
Sires ⟶ Sons	35%	41%	34%
Sires ⟶ Daughters	11%	10%	8%
Dams ⟶ Sons	49%	45%	49%
Dams ⟶ Daughters	5%	4%	9%

The response to selection (Re), or genetic gain, per year can then be estimated from the formula $Re = (r_{AI} . i . \sigma_A)/y$. The value of σ_A is given; it can be changed over the generations but at a certain time we must accept it as it is. The other three terms on the right side of the equality sign are at least partly under the breeder's control. The accuracy and the intensity of selection can be increased, and the generation interval can be decreased, thus increasing the selection response per unit of time. It is possible to estimate the contribution of a certain change in each one of these three factors to the total selection response.

Let us assume that we select for higher milk yield only in the breeding of dairy cattle. The first part of Table 3 presents estimates of the genetic progress which it should be possible to obtain per year under optimum structure of the breeding population. Only the milk-recorded cows contribute actively to the progress, but the non-recorded cows will be improved along with the recorded although at a somewhat slower rate. Three different population sizes are considered, comprising 2,000, 20,000 and 40,000 milk-recorded cows, respectively. According to the calculations, the progress, expressed as a percentage of the average yield of all the cows, would be 1½ times as rapid in a population of 20,000 milk-recorded cows, as when the number is only 2,000. Part I of the table shows also the relative contribution of the parents of the next generation to the total

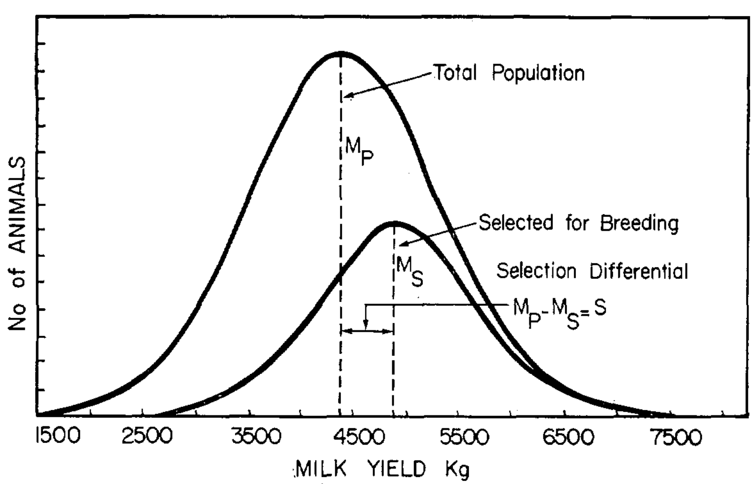

FIG. 1: *Selection for milk yield in cattle.*

genetic progress. The greatest contribution is made by the sires of new bulls, assuming that all these bulls are progeny tested and efficiently selected, and their contribution increases with increasing size of the population (43 to 62%). It is assumed that about 50% of the sires of cows are progeny tested, the other 50% being young bulls used for progeny test. However, this percentage would normally decrease with increasing population size. Their combined contribution is about 18% of the total. The selection of dams of new sires contributes 33 to 23% to the total genetic gain, decreasing with increasing size of the population. The effect of selection of dams of daughters is low throughout, depending on the fact that this selection never can be very efficient since at least 50% of the heifer calves must be raised in order to keep the cow population constant in number.

Part II of the same table shows the genetic improvement with regard to milk yield which probably has been achieved during stated periods in Norway and Finland within their most numerous breeds, estimated from actual selection differentials and generation intervals. The estimated progress is only 0.8 to 1.0% of the breed averages. There are several explanations for this. Selection has been made for several traits at the same time, for example, body size, ease of milking and udder shape, although milk yield has been considered most important. Furthermore, not enough young bulls have been progeny tested in order to provide an efficient selection. In Finland, for example, about every third tested bull was approved as bull sire and every second as cow sire. The generation interval has also been rather long. In Finland, the average age of the bull sires at the birth of their sons was 9.3 years and that of bull mothers was 8.7 years. The average age of cow sires at the birth of their daughters was 6.2 years and that of cow dams was 5.9 years. However, in recent years the length of the generation interval has been decreased; especially is this the case in Norway.

SELECTION OF SIRES AND DAMS FOR BREEDING

Since the selection of sires is likely to be the strongest force in the improvement of a cow population, the organization of bull progeny testing and selection are of paramount importance. An attempt must be made to find the optimum balance between the number of bulls (m) that should be tested per year and the number of daughters with first lactation records that should be required for the progeny test of each bull (group size = n). Testing few bulls on many daughters each means high accuracy of the individual tests but little choice among the tested bulls — *i.e.*, small selection differential. On the contrary, testing many bulls on few daughters each means low accuracy of the tests but high selection differential.

Robertson (1957) has analysed this problem and derived a formula for its solution. He introduced the term "testing ratio" (K) = N/S where N = testing capacity — *i.e.*, the number of daughters of young test-bulls which all complete a first lactation record — and S = the number of tested bulls that will be selected for breeding. Further, h^2 = the heritability of the first lactation milk yield. Then he finds that, when $K/a > 3$, the optimal group size approximates closely $n = 0.56\sqrt{(K/h^2)}$. The correlation between the breeding value of the bull and his progeny test on n daughters (I) is

$$r_{AI} = \sqrt{\left\{\frac{n\,0.25h^2}{1 + (n-1)0.25h^2}\right\}}$$

$= \sqrt{[n/(n + a)]}$ where $a = \sqrt{[(1 - 0.25h^2)/0.25h^2]}$. The heritability of the progeny test (= the regression of future daughters on those tested = b) is r^2_{AI}.

Figure 2 shows how the heritability of the progeny test and the phenotypic and genetic selection differentials

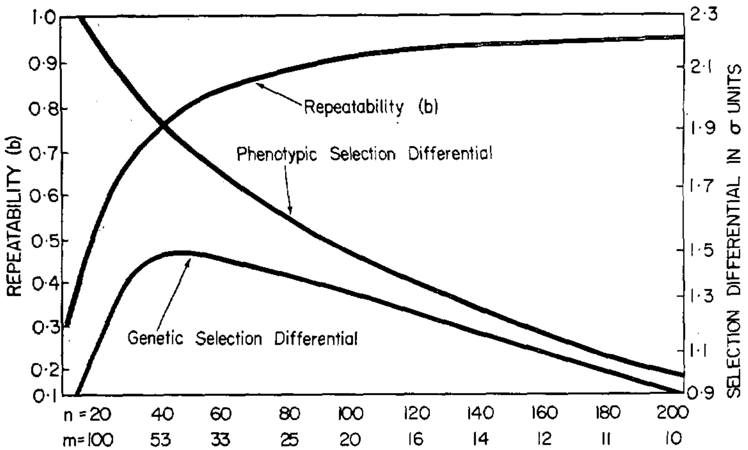

FIG. 2: *Influence of number of bulls tested and number of daughters (testing capacity constant) on heritability of progeny test and selection differentials (refer to text).*

expressed in standard deviation units, are influenced by the group size (n) when the testing capacity is held constant at a total of 2,000 milk-recorded daughters. In this case the optimal group size is about 40 daughters per bull with a tolerable range of 25 to 60 daughters. With n = 40 it is possible to test 50 bulls per year. About 80% of these bulls will probably still be active when the progeny test is completed. If the two best of these bulls are selected for the breeding of new bulls, as recommended by Skjervold (1967), the selection differential will correspond to 2.1 standard deviations of the breeding value of tested bulls. The next best (10 to 20%) of the tested bulls can be used for breeding cows.

The dams of bulls are chosen mainly on their own performance and their sire's progeny test. According to Part II of Table 3 the contribution of the dams to their sons' breeding value has been more important than the contribution of the sires of the young bulls. However, this may be an overestimate. Vos and Politiek (1964) analysed data for 110 progeny-tested Dutch Friesian bulls and their dams and sires. The correlation between the progeny test of sires and sons (for milk yield) was 0.49 ± 0.07 whereas that between the dams' own yield and their sons' progeny test was only 0.06 ± 0.10. In England, O'Connor (1963) analysed a sample of 736 progeny-tested Friesian bulls and their 640 dams, calculating the regression of the sons' progeny test on their dams' own milk yield and butterfat percentage. Where possible the first five lactation records of each dam were included, separately and combined to an average. It was found that, while the regressions for fat percentage were in agreement with those expected on theory, the regression for milk yield for second and subsequent lactations, as well as for the average of all lactations were insignificant. The only significant correlation for milk yield was obtained from the dams' first lactation record and the progeny test of their sons. There are probably three reasons for this finding:

(1) That the heritability of the first lactation record is relatively high according to most investigations.

(2) That when a cow in a breeding herd has done relatively well in her first lactation she is considered as a prospective bull mother and therefore better fed and cared for than the other cows in the herd.

(3) That all bull mothers are highly selected animals and therefore show relatively little genetic variation.

If selection is for milk yield only, it might be preferable to consider only the first lactation yield of presumptive bull mothers, but when also such traits as mature size, persistency of yield, and normal reproductive behaviour enters into the selection it would be necessary to postpone the decision until two or three lactations are completed, although it increases the dam-son generation interval. However, it is unlikely that the common formula for the heritability of an average of several lactation records is applicable.

The generation interval between sires and sons can be reduced by an early progeny test and a rapid turnover of the tested bull sires. If the test inseminations of young bulls are completed when they are about 15 months of age, and the daughters calve at 24 to 27 months of age, the progeny tests are completed when the bulls are 5 to 5¼ years old. That this is possible under A.I. breeding is shown in Norway, where the average age of the bulls at the completion of the test was 5.2 years in 1967. If the selected bull sires are used only one year, or at most 2 years, the generation interval between sires and sons will be 6½ to 7 years. On an average, nothing is gained by using the tested bulls throughout a number of years, except perhaps in very exceptional cases. The generation interval between sires and daughters would on an average for tested and untested sires be 4 to 5 years, and the interval between dams and offspring would be about the same.

THE ORGANIZATION OF A.I. BREEDING IN NORWAY

In Holland, West Germany and the Scandinavian countries, no beef breeds are kept except on a small scale for crossbreeding purposes. The modern trend is to improve the dairy breeds, not only for milk but also for beef production. This trend has been most pronounced in Holland and West Germany where the type of Friesian cattle has been changed in the last 30 years to a dual-purpose type, distinctly different from the Holstein-Friesian type of North America. Bulls, steers and heifers of the modern Friesian breed show higher growth rate and produce at least as large a proportion of lean meat as the specialized beef breeds, and the general quality of the meat seems to be just as high.

The dairy cattle breeding in northwestern Europe is rapidly proceeding on the road to centralization of practically all improvement activities. This development is especially marked in Norway. The general scheme which is applied there may be outlined as follows:

(1) The cow testing records are accumulated and processed at the central office of the A.I. organization. All records are converted to milk with 4% fat and expressed as deviations from the contemporary herd average. Then a selection index is calculated for each cow, based on her own record, the progeny test of the sire and the performance of her dam. On this index, about 3% of the cows are selected for insemination by semen from elite bulls. A second selection is then made among the bull calves from these inseminations, based mainly on further information on the dams, accumulated during the preceding lactation and comprising ease of milking, conformation (mainly udder and teats), and reproductive performance. Usually, the third or fourth calf from an elite cow is chosen in order to keep the generation interval relatively short.

(2) Each year 200 to 250 bull calves from the elite matings are selected and brought to a central rearing station where they are raised in a standardized environment suited for young growing animals. When the bulls have reached one year of age, a selection is made on growth rate, conformation and sexual behaviour, and about 50% of the total number are selected and divided between two A.I. stations for progeny test.

(3) Semen from each one of the selected young bulls is used for insemination of about 700 cows in milk-recorded herds in order to obtain about 100 daughters which complete their first lactation. In this progeny test other traits of the daughters are also considered (ease of milking, conformation and reproductive performance).

(4) The bulls are progeny tested also for growth rate and carcass quality. A random sample of at least 8 bull calves from each bull is raised at a special testing station until the animals reach suitable development for slaughter at about 18 months of age. Carcass records are taken according to a certain scheme.

(5) Following the inseminations for progeny test, 12,000 to 15,000 insemination doses are harvested from each bull, deep-frozen and stored in order to provide for 6,000 to 7,000 pregnancies after completion of the progeny test.

Then the bulls are slaughtered at about two years of age and their value for meat production is determined. In Finland, it has been calculated that the cost of keeping deep-frozen semen in storage for about four years amounts to only about 25% of the cost of keeping the bulls as "lay-offs".

The selection of the bulls is made at three stages:

(1) The first selection is made on the pedigree (elite sire and dam) and on the development of the bull calves.

(2) The second selection is based on the performance test of the bulls at the raising unit, including growth rate, conformation and sexual efficiency.

(3) The third and final selection is based on the progeny tests for dairy and beef qualities, and also on the performance test for body development and carcass quality of the bulls at 24 months of age.

On the basis of the third selection the bulls are divided into four groups:

(1) *Elite bulls* (the two or three top bulls in each batch of about 100 tested) which are used primarily on the elite cows for production of new bulls.

(2) *A-bulls,* the 12 next best of the tested bulls to be used on the production tested cows which are not mated to young bulls (about 50% of the active cow population).

(3) *B-bulls,* with a ranking of 14th to about 40th of the tested bulls, are used for breeding non-tested cows.

(4) *The rest of the tested bulls* (about 60%) are culled (semen discarded).

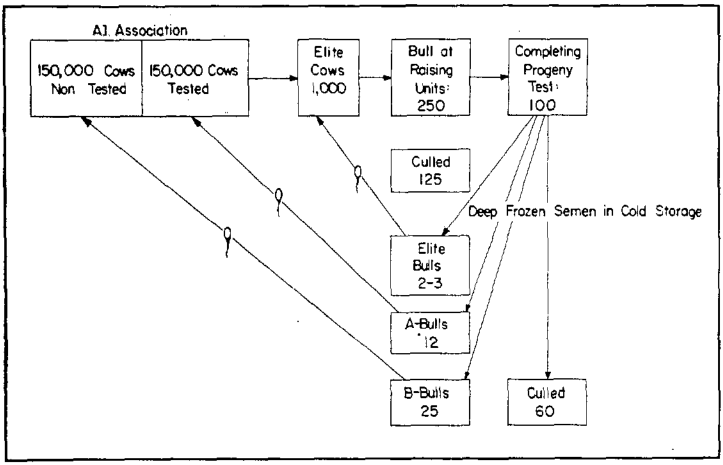

FIG. 3: *Dairy cattle improvement scheme — Norway.*

Figure 3 gives a summary of this general scheme which is now applied in practice. All inseminations by semen from tested bulls would be made within a period of one year or a little more. Skjervold (1967) estimates that this programme would yield about 90% of the genetic progress which is theoretically possible.

Planned matings for bull production and central raising of the bull calves was started in England by the Milk Marketing Board several years ago and it is now adopted not only in Norway but also in Sweden and to some extent Finland and Holland. It is combined with early progeny testing and intensive selection among the tested bulls. According to my estimation these measures will prove to be of great value in dairy cattle breeding. Obviously, the young bulls can be much better compared when they are raised centrally in a standardized environment than when they are raised by private breeders and later sold to the A.I. organizations. The Norwegian system of storing large quantities of deep-frozen semen of the young bulls for later use, several years after the bulls are slaughtered, may need further proof of its advisability. According to investigations by Dr G. W. Salisbury, University of Illinois, significantly higher return rates are obtained when deep-frozen semen is stored for 18 to 24 months than after shorter storage. The implication is that not only relatively more spermatozoa are incapable of fertilization but also that the early embryonic mortality increases. This is a problem which needs further investigation.

COMMENTS ON THE SELECTION PROCEDURES

The selection of dairy cattle in the Scandinavian countries is now carried out strictly from a utility point of view, and the "formalism" which was fostered during the first decades of this century has gradually disappeared. The selection pressure is concentrated on the economically most important characters, and at present those are the yield of milk and beef with about equal weight on each. Other important traits are fertility, ease of milking, udder proportions, and size, shape and placement of teats. Some other traits may also need consideration, for example, negative deviations in body build, especially with regard to legs and feet.

The question may be raised to what extent selection indices should be calculated and used. As a personal opinion, I would say that such indices have their greatest value when used for quantitative traits with a fairly wide range of tolerable variation, and when it is shown that these traits are genetically correlated. Such traits as the calving interval and services per pregnancy of individual cows have so low heritability that it is of no use to include them in a selection index. I think it is better simply to exclude cows with poor reproductive records from the breeding group, and the same would apply to progeny-tested bulls with high return rates. Similarly, cows with poor udders and pronounced defects in body build, legs and feet should be excluded. Their frequency is relatively low in our cow populations. With regard to ease of milking, neither extreme is desirable. Slow milkers do not fit in with the regular milking routine, and cows with a poor closure of the teat sphincter show a lowered resistance to mastitis. Therefore, extreme deviates in both directions may be excluded from breeding.

Investigations so far do not show any significant genetic correlation between milk yield and growth rate of the animals. If there is any correlation at all, it is slightly positive. But most likely, there is a negative correlation between "beef type" and milk yield (Table 2), when "beef type" is characterized by a low-set, short and broad body. However, the modern rapid-growing dual-purpose cow should neither be very short in the body nor excessively low-set but have plenty of frame with good muscular development. The heritability of growth rate and body size at maturity is a little higher than that of milk yield per lactation but the difference is not very pronounced. Therefore, one standard deviation in growth rate and in milk yield would add equally to the breeding value of the animal. The construction of breeding indices would be needed, particularly when, for example, the breeding value of presumptive bull mothers is rated on the cow's own performance as well as on pedigree information.

CONCLUDING REMARKS

The spread of A.I. has made it possible to organize the breeding procedures for large units, which is a prerequisite for a rational production and raising of young bulls as well as an efficient progeny testing and selection among the tested bulls. The electronic computers take care of the registration of pedigrees and performance records, the progeny tests and the first selection of dams of new bulls. Any cow with excellent records and other required qualities may be used as dam of bulls whether she is purebred or not in the traditional sense of the term. The majority of dairy farmers today are more interested in an economical production of milk and meat than in pedigree certificates covering many generations of ancestry. In modern animal breeding, the activities are centralized, and the planning and decisions are to a large extent made by experts. There has been some fear that the centralization may have a destructive effect on the interest of the practical farmers in the improvement of their cattle but the experience so far does not verify this. The great majority of dairymen are quite willing to co-operate.

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