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SYMPOSIUM REGIONAL SUR L'AMELIORATION GENETIQUE DES BOVINS SOUS CLIMAT SUD MEDITERRANEEN
Tunis, 20 - 23 Novembre 1989

REGIONAL SYMPOSIUM ON GENETIC IMPROVEMENT OF CATTLE IN THE SOUTHERN MEDITERRANEAN CLIMATIC CONDITIONS
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INTRODUCTION

Milk and dairy products constitute an important part of the human diet in almost all parts of the world. In European countries, consumption per head approaches one litre of milk equivalent per day. In Latin America it is generally about one third of that, while consumption levels are lowest in Asia and Africa at about one tenth of European levels. In the developed world total dairy production has been increased so successfully that there is now a general surplus to market requirements. Throughout the developing world, on the other hand, total production is generally increasing annually, and will undoubtedly continue to increase for many decades into the future.

A major component of the technical revolution in dairy production in the developed countries in the last forty years has been the remarkable genetic improvement in output potential per cow. Combined with improvements in feeding and husbandry, this has led to a doubling of production per animal in many countries over the last thirty years. The engine which has driven this genetic improvement has been the effective selection of bulls for use in artificial AI, and the effectiveness of this selection has in turn been based on well-planned, organised and executed progeny testing.

My purpose in this paper is to review briefly the evolution of modern progeny testing methods, and to discuss their application in the context of the widely varied structure in today's cattle populations.

WHY PROGENY TESTING?

The central place of progeny testing in modern dairy improvement programmes owes its predominance to the following factors:

- the traits of interest, all connected with milk production, can be measured directly only in females. Bull selection must therefore depend on information from female relatives
- The spread of artificial insemination has meant that individual bulls can have an enormous impact on the population. It is therefore imperative to know their genotype with some precision. At the same time, through AI, large numbers of daughters can be measured

The simplest formula for genetic gain is:

Gain = (accuracy of selection) x (intensity of selection) x (genetic variance)

The genetic variance is a function of the evolutionary history of the population, and not something which can easily be modified. The intensity of selection can, of course, be increased by testing more animals for each one selected. It is therefore largely a question of how much money is spent on the testing exercise. The third factor, the accuracy of selection, depends on the heritability of the trait or traits included, and on the number and relationship of the relatives measured for each candidate for selection.

The main dairy production traits have a heritability in the region of 0.2-0.3. The accuracy then depends on the number and relationship of the relatives. The measure of accuracy used is the correlation between the information used for selection on the one hand, and the candidate's true genetic value on the other. This correlation is shown in table 1 for different combinations of relatives.

From this it is clear that even a modest number of progeny gives a more accurate evaluation of animals to be selected than any combination of information on the animal itself, on its full or half-sib contemporaries, or on its ancestors. This is the essential reason for the central place of progeny testing in modern dairy cattle AI programmes.

Table 1: Relative accuracy of selection for different sources of information ($h^2 = 0.3$)	
Information on	Accuracy %
Self	55%
Parents	39%
Complete pedigree	45%
4 full sibs	45%
40 half sibs	44%
10 progeny	70%
40 progeny	87%
120 progeny	95%

CONFLICTS

In the use of progeny testing as a basis for selection, two important conflicts need to be resolved. The first is a possible conflict between intensity of selection on the one hand and accuracy of selection on the other. Clearly, the more progeny which are recorded, the more accurate the progeny test. However, if there is some limit on the total number of progeny records which are available, then higher accuracy (ie more progeny per bull) implies a fewer number of bulls tested, and consequently a reduced selection intensity. Resolution of this conflict has been explored by Skjervold and Langholz (1964). The optimum combination of accuracy and intensity will differ in different populations. However, in most programmes a minimum of 50 progeny is required.

This conflict is not particularly acute in some countries which have very high levels of milk recording, and consequently very large numbers of potential progeny records. It is most difficult to resolve in those countries where commercial milk production is in the early stages of development. This generally implies a preponderance of small herds, and relatively low yields per cow, which do not produce the economic output to justify the infrastructure of a recording system.

The second potential conflict is between accuracy of progeny testing on the one hand

and generation length on the other. The expression for genetic gain given above is gain per generation. This must be divided by the generation length to give gain per year. The longer the generation length, the slower the gain per year. With progeny testing in dairy cattle, bulls are normally at least five years old before a final selection can be made. As an alternative, they could be selected for use at a year of age, though at greatly reduced accuracy since this selection could only be based on information from female ancestors and sibs. This conflict was first examined by Dickerson and Hazel (1944). They concluded that in a swine population the losses from a longer generation interval more than offset the gains from increased accuracy of progeny testing. They therefore recommended that selection should be based on own individual performance records and that progeny testing should not be used.

With the development of embryo transfer in cattle, the potential number of offspring from outstanding cows can be increased greatly. Nicholas and Smith (1983) re-examined the trade off between generation interval and selection accuracy in these circumstances, and concluded that a properly structured selection scheme without progeny testing could achieve a higher rate of annual genetic change than the conventional schemes which rely on progeny testing. They applied the name MOET (Multiple Ovulation Embryo Transfer) to such a scheme and a number of versions of this programme have now been put in place in Europe.

One way of extending the testing capacity of a population is of course to devote a higher proportion of the inseminations to young bulls rather than to proven bulls. Much work in the early 70's was devoted to exploring optimum population structure in this regard. In general, it was concluded that anywhere from 25 to 50% of the population should be bred to young bulls. A large part of the justification for this conclusion was that most of the genetic gain came in the sire to son path in the classic 4-path model first described for dairy cattle population by Rendel and Robertson (1950). However, for dairy traits, economic benefits from selection are realised only in females. Genetic gain transmitted to males is, in effect, put into storage for one generation, and only exploited when these males in turn pass it on to the next generation of females. When this economic dimension is taken into account, the relative importance of the sire to son path is greatly decreased, and that of the sire to daughter path (ie the commercial inseminations) is greatly increased.

One consequence of the emphasis on the sire to son path was that it was not regarded as important to have heavy usage of selected bulls: their main contribution to genetic progress was through their sons. As a result, it became common, for financial reasons, in some countries to slaughter young bulls once a certain store of semen had been accumulated.

However, the economic model says that heavier use should be made of young bulls and there is now a tendency in most programmes to keep young bull usage to less than 20% of all AI.

EFFICIENCY OF PROGENY TESTING STRUCTURES IN DIFFERENT POPULATIONS

Western Europe with 25 million dairy cows and North America with 12 million have both developed many sophisticated AI-linked breeding programs.

A few years ago, I looked at this in some detail (Cunningham, 1982). These different programs vary in about fifteen separate aspects, including such things as scale of investment in young bull purchase and testing, level of usage of selected bulls, proportion of inseminations carried out by young bulls, relative importance of different traits, rate of turnover in the bull stud, rate of turnover in the cow population, etc. We consider the first two to be the most important. The results are summarised in **Figure 1**. This shows 30 large scale AI programs, plotted by number of bulls progeny tested per million AI and by estimated lifetime use of selected bulls. The backround lines represent equal rates of estimated genetic gain.

What we find is that of the thirty breeding programs examined, the European ones tend to be quite distinct from those in America. The basic difference is that European populations invest much more heavily in acquiring, testing and selecting among young bulls (up to 450 bulls per million AI). However, lifetime usage of the selected bulls tends to be quite low. In America, investment is much less (less than 100 bulls tested per million AI), but selected bulls are very heavily used.

These differences can be fairly easily rationalised. Most of the European organisations are cooperatives, ready to make major investments on behalf of their members, while the American industry is dominated by commercial companies which invest with much greater prudence. The British and Irish programs are the exceptions in Europe, tending to look more like American organisations in their breeding structure.

The lessons from these comparisons are fairly obvious. Some of the European populations have invested excessively in their testing programs, and could get better value for money by increasing bull usage. The American organisations could been accumulated.

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The lessons from these comparisons are fairly obvious. Some of the European populations have invested excessively in their testing programs, and could get better value for money by increasing bull usage. The American organisations could probably benefit by increasing the investment in testing.

METHODS

The history of progeny testing methodology has been reviewed by Pirchner (1984). These methods began in the 1930's, and were developed extensively from 1950 onwards, as their application in artificial insemination became widespread. The problem they addressed was in all cases the same: how to refine the data in such a way that the progeny averages were an unbiased and precise measure of the sire's genotype.

The methods developed in different countries tended to converge over the years. Their successful application also produced a significant new problem: because genetic change was being achieved, bulls of different ages or origins being compared at any one time were likely to be from distinctly different genetic groups. Furthermore, the traditional methods were incomplete in the sense that they did not take account of the network of relationships which build up between bulls in a population.

In order to resolve these two difficulties, as well as to give theoretically optimum estimates of breeding value, Henderson (1973) proposed a new system which he called BLUP (Best Linear Unbiased Prediction). In recent years, it has been almost universally introduced in modern dairy cattle breeding programmes, and under the name "animal model BLUP" has been extended to simultaneously evaluate all animals in the population, not just the sires being progeny tested.

The development and application of BLUP has been made possible by the simultaneous evolution of statistical theory, computing algorithms and computer power. With the internationalisation of so much breeding material now, the next challenge is the effective linkage of evaluations from different programmes.

COSTS AND BENEFITS

How relevant are these sophisticated progeny testing and selection programmes in countries with developing dairy industries? The first point is to recognise that, to be effective, such programmes must have a certain minimal scale. The original progeny testing programme in Cambridge, for which Rendel and Robertson (1950) developed the contemporary comparison method, was designed to progeny test 4 bulls per year and to select one for general use. At that time and in those circumstances such a programme made sense. It did not face competition from more high powered programmes elsewhere. Today, such a programme would make no sense at all. In Europe alone, there are about 30 separate AI related progeny testing and selection schemes. Most of them are designed to serve populations of at least half a million cows, and most of them progeny test at least 100 bulls per year. Two thirds of them relate to Holstein/Friesian cattle, and these all have access to the same genetic materials. A small scale isolated programme has very little chance of being able to match the genetic quality of the bulls coming from these larger programmes.

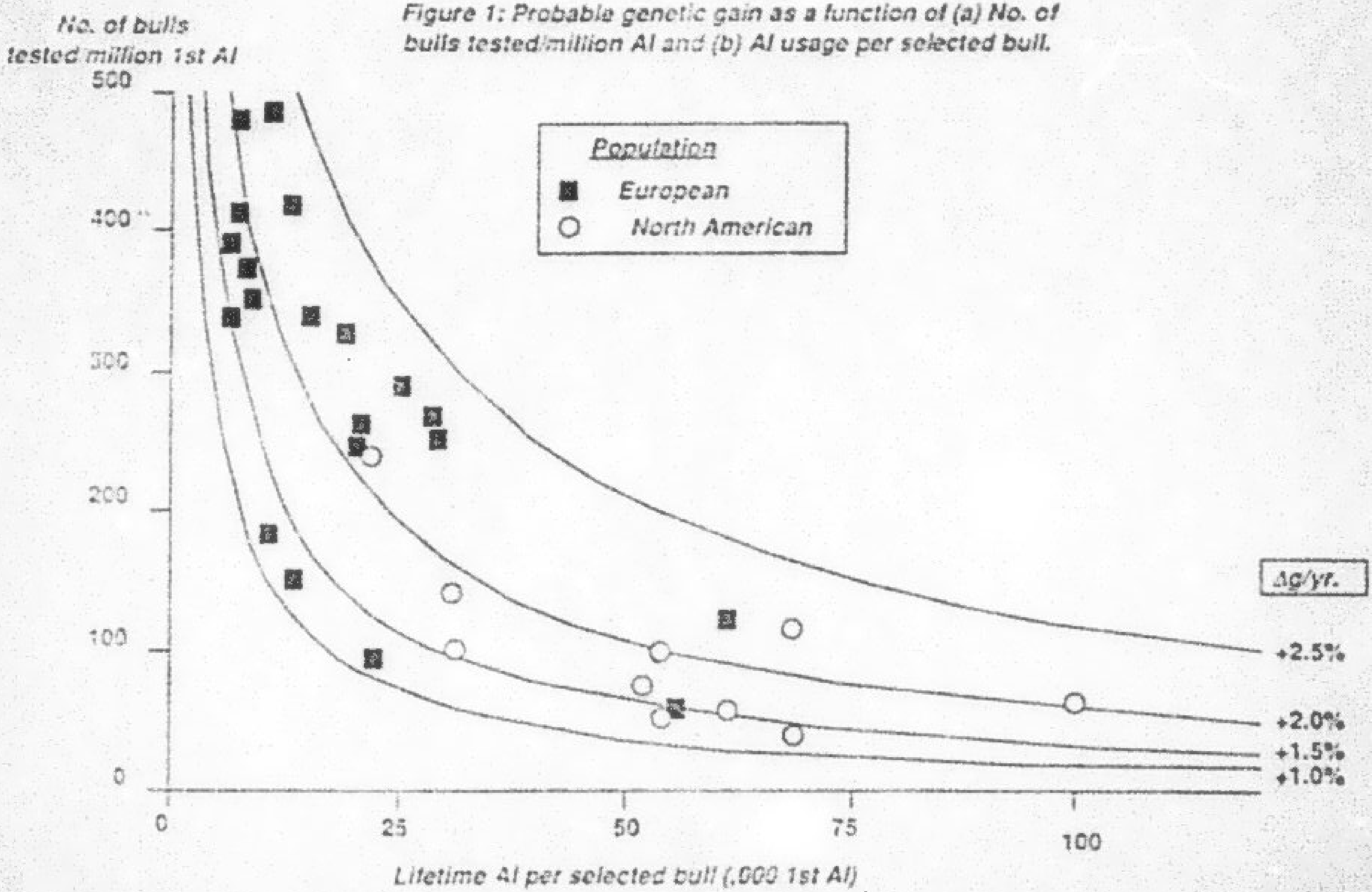
Furthermore, these programmes are enormously costly. **Table 2** shows the estimated costs of progeny testing a single bull in each of a number of European countries. Costs differ largely because in some populations the generation of the progeny data is paid for through the normal milk recording process, while in others specific incentives are needed to generate the progeny records. However, it can be seen that, in general, a figure of about $25,000 per bull progeny tested applies. Given that selection intensities range from 1 in 5 to 1 in 10, the cost per bull selected in these programmes then ranges from $125,000 to $250,000. To repay such an investment requires that the selected bulls be used on a very large scale. This, again, militates against the prospects for a successful progeny testing programme in small populations (defined as the number of cows bred by AI).

The primary circumstances which would justify a separate breeding programme in spite of small size, modest use of AI, and poor recording infrastructure, would be the situation where the selection objective was significantly different from that pursued by the larger programmes. This is primarily a question of genotype by environment interaction. Do genotypes rank the same in circumstances which support more than 5,000 kg of milk per cow and in those where average production levels are less than 3,000? We have insufficient evidence on this question.

Table 2: Approximate costs of progeny testing bulls in some European countries.

COUNTRY	COST/BULL PROGENY TESTED
	--- $ US ---
Netherlands	39,000
Denmark	22,000
Norway	21,000
Finland	10,000
France	46,000
Ireland	23,000

Figure 1: Probable genetic gain as a function of (a) No. of bulls tested/million AI and (b) AI usage per selected bull.



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