
VOLUME 62 2002

Cornell Research on Methods of Selecting Dairy Sires

C. R. HENDERSON, Cornell University, U.S.A.

INVESTIGATIONS by the Department of Animal Husbandry at Cornell University of sire selection methods have included two phases, first the use of natural service progeny tests and more recently the employment largely of artificial insemination progeny tests. This report discusses only the second of these, primarily because it has been more productive of concrete results. These findings represent the joint efforts of several of my colleagues and myself. I should especially like to acknowledge the contribution of my former graduate students, R. S. Dunbar, C. G. Hickman, and R. L. Blackwell, and Cornell Dairy Extension specialists H. W. Carter, R. W. Spalding, R. Albrectsen, and S. W. Brownell. The financial support and encouragement of the New York Artificial Breeders' Co-operative (NYABC) is also gratefully acknowledged.

Advantages of A.I. Progeny Tests for Genetic Research.

Natural service progeny tests have two serious deficiences for genetic research. First, the number of progeny per sire is small, and second, all progeny of the sire are usually located in a single herd. Consequently sampling errors are large and it is not possible to disentangle the influence of the genetic merit of the sire from the feeding and management and genetic influence of the herd. In contrast, bulls used in A.I. have many recorded daughters scattered in almost as many herds, and contemporary daughters of several bulls are recorded in the same herd. Further, in the absence of nominated services the breeding value of the sire is uncorrelated with the environment and the genetic merit of the herds in which he is used. Consequently by use of appropriate statistical techniques the sire effects can be separated from the herd effects.

Cornell Facilities for Research in Sire Selection.

Research workers in dairy cattle breeding of the New York State College of Agriculture at Cornell University are fortunate in having the bull stud of the state-wide artificial insemination co-operative located at the college. Extension and research personnel assist the Co-operative in the selection of its sires, and though the final decision regarding the purchase of a sire rests with the Co-operative, any reasonable requests aimed at furthering the research programme are granted. The Co-operative's team of bulls numbers about 120, somewhat over half of which are young bulls being held until their first A.I. daughters' production records become available. These bulls provide semen for nearly 400,000 first services per year resulting ultimately in more than 10,000 new first lactation records per year.

The production records of A.I. daughters as well as the records of their herd mates provide most of the data used in our sire selection research. Herd recording is carried out under the direct supervision of our extension specialists. When each lactation is completed, the testing officer submits to the extension office certain pertinent data including total milk production, butterfat test, age of cow at freshening, length of lactation, heart girth measurement in the second month of lactation, and identification of parents. These data are checked and transferred to an IBM card ready for routine sire evaluation or for dairy cattle breeding research.

The Department of Animal Husbandry has its own IBM installation for analysing production data. Funds for the rental of these machines are provided by NYABC with the understanding that progeny test results of the Co-operative's sires will be compiled regularly and that assistance will be given in assembling data suitable for evaluating prospective A.I. sires. In the considerable time remaining apart from these requirements the machines can be used for any research in dairy cattle breeding thought by our staff to be most promising.

Estimation of Basic Parameters.

One of the first uses made of A.I. progeny test results was the estimation of certain parameters, the values of which were needed as a guide in planning research and in developing operational procedures for the guidance of sire selection committees of NYABC. Periodically as more data, more powerful statistical techniques, and faster machines became available these parameters were re-estimated and others were investigated for the first time. In gneral these estimations have involved the partitioning of the total variance of records of A.I. daughters by variance components analyses. Methods applicable to unequal subclass numbers have been developed in connection with this work, Henderson (1953). The most recent analysis by Hickman and Henderson (1955) showed the following contributions to the total variance of 305-day records corrected to maturity by multiplicative factors.

Sire	7%	7%
Herd	30%	33%
Year and Season	4%	5%
Sire x Herd	2%	2%
Herd x Year and Season	14%	15%
Residual	43%	38%
	6,673,000lbs.[2]	8,606lbs.[2]

Evaluation of Sire by A.I. Progeny Records.

As soon as A.I. daughters' records became available we were faced with the problem as to how they should be used to estimate the true value of the sire. This information was needed to decide, first, whether the bull if still alive should be continued in A.I. and second, whether his sons or grandsons should be considered for selection. Also we needed some accurate procedure for comparing groups of bulls selected by different methods. Research on the problem of interpreting A.I. progeny tests is still in progress, but some of our results to date are described below.

Appraisal of Trends in Production of A.I. Daughters.

After several years' production data had accumulated it became apparent that marked year to year changes were occurring, from 400 pounds to 445 pounds between 1947 and 1949 for example, Carter and Henderson (1955). The important question was, how much of these fluctuations was due to changing genetic merit of the bull stud and how much to other factors beyond the control of those selecting sires for A.I. The problem was investigated by a maximum likelihood technique analagous to that described by Henderson (1949) for estimating environmental trends in individual herds. Only first lactation records were used because of the possibility of bias resulting from incorrect age factors. The result of this analysis was that we find no evidence of any change in the merit of the bull stud. Consequently all annual changes should be taken into account when comparing bulls whose daughters do not freshen in the same years. For a time we did this simply by adjusting each record according to the amount by which the average of all A.I. records for that year differed from the long-time average. The problem of causes of trend will need to be re-investigated when the progeny of sires selected by our newer selection procedures come into production.

Seasonal Influence on Records.

Another source of error in A.I. progeny tests became apparent, namely the month of calving, Hickman and Henderson (1955). It has been well known that autumn freshening cows in the U.S. produce considerably more than those freshening in the spring. Our A.I. data confirmed this finding and further the proportion of autumn freshening daughters varied significantly among bulls, particularly for the first 100 daughters. This disproportionality is simply a consequence of when the bull is first used in A.I. We found that under New York conditions a major part of the variation due to date of calving could be controlled by classifying the lactation either as autumn freshening (September 1st through February) or as spring freshening (March 1st through August). Instead of adjusting records for the overall seasonal average we decided, because of our large estimate of herd by year and season interaction (14 or 15 per cent of the total variance), to adjust for seasonal effects separately by herds, employing a technique similar to the N.Z. Dairy Board's "expectancy" method.

Relation Between A.I. Record and the Contemporary Herd Average.

Our estimate that herd and herd x year and season account for nearly half of the total variation in A.I. daughters' records warned us that herd differences contribute an important random error to progeny averages based on relatively small numbers and could constitute a serious bias if there were any selection by the herd owner of the bulls he uses. We were particularly concerned that more young bulls might be used in lower producing herds than proven bulls and that young bulls with "popular" pedigrees might be selected for use in better than average herds. Although NYABC does not have a "nominated mating" programme, the technician does carry the semen of two or three bulls of each breed from which the dairyman can practice limited selection if he wishes. It was decided therefore to estimate the regression of A.I. daughter production on the mature equivalent average of her herd mates that freshened in the same year and season. Herd sizes are too small in New York to limit the comparison to the mature cow average as is done in New Zealand. Our estimate of the above regression was .60, a value somewhat smaller than we expected, Henderson, Carter and Godfrey (1954). Since it was thought that erroneous age conversion factors might bias the estimate downward, the regression was re-estimated using for comparison the production of cows of the same age and freshening in the same year and season as the A.I. daughter. The estimate was again .60. In both cases an adjustment for number of contemporary records was employed. The procedure used at present at Cornell for adjusting the individual A.I. progeny for herd, year and season is as follows:—

$$\text{Daughter record } \frac{.6n}{n+1} (\text{contemporary average} - \text{breed average})$$

where n is the number of contemporary records.

Adjustment for Number of Recorded Daughters.

The primary purpose of an A.I. progeny test is to rank bulls as accurately as possible so that decisions can be made about which ones to continue in service and which ones to provide sons and grandsons for future use in the breeding programme. If all sires had the same number of recorded daughters each with the same number of lactations, the progeny averages adjusted for age, contemporary herd averages, etc. rank the bulls as accurately as possible. But when these numbers vary, some account needs to be taken of this fact. For example, which bull should be preferred, one with 20 daughters averaging 30 pounds more than the breed average or one with 100 daughters averaging 20 pounds above the mean of the breed? From our data we find that for single lactation daughters an almost optimum ranking procedure is

$$\frac{n}{n+12}$$

(daughter average—breed average) where n is the number of recorded daughters and where the daughter average is adjusted for those factors described above. Modifications of this procedure improve the ranking somewhat when the number of records per daughter varies.

Validity of Selection Based on First Lactation.

One of the criticisms frequently made of sire selection based on progeny tests is that over-emphasis is automatically placed on first lactation records with consequent selection for early maturity. Even if this were so, it is not certain whether this is a bad thing; but our work indicates that the daughters of different A.I. sires vary little with respect to increase from first to second lactation, Hickman and Henderson (1955). From this we concluded that the heritability of rate of maturity, as measured by production, is low.

Sire Selection by Sampling in A.I.

Our estimate that sires make a substantiatl contribution to variation in A.I. daughters' production encouraged us to investigate the potential genetic gains from A.I. sampling tests, Henderson and Dunbar (1952). Also by this time it had become apparent that we had been unable to predict at all accurately A.I. progeny from the natural service progeny test. We concerned ourselves primarily with estimating the genetic merit of bulls selected on the basis of their A.I. daughters as compared to the average merit of all bulls sampled and studying the consequences of different numbers of bulls sampled and of different numbers of recorded daughters per bull. The solution to these problems depended on:—

1. The variation in true merits of sires selected for sampling.
2. The number of bulls sampled.
3. The number of bulls selected on the basis of the sampling test.
4. The accuracy with which the sampling procedure ranks bulls.

The standard deviation of the true daughter average had been estimated by Hickman and Henderson (1955) as approximately 25 pounds butterfat. The accuracy of the sampling test in evaluating bulls can be expressed as the correlation between the estimate of the bull and his true value. This was estimated as

$$\sqrt{\frac{n}{n+12}}$$

where n is the number of daughters, with one record each. It can be seen that this correlation approaches one rapidly as n increases. Now clearly, for some specified number of A.I. daughters resulting from the sampling programme, increasing n will improve the accuracy of ranking but will permit fewer sampled bulls from which to select. Thus there is some optimum number of bulls to test in any particular situation. The following table taken from Henderson (1954) illustrates this point as well as indicating the expected gains to be derived from a sampling programme. The figures in the body of the table represent the expected superiority in pounds of butterfat per year of the daughters of bulls selected by sampling as compared to daughters of bulls put into service without preliminary sampling. The assumption in these calculations is that 5 bulls are needed for replacement in each cycle of sampling and that 20% of the bulls die or become unfit for A.I. service before production records become available.

No. of bulls sampled	Total Number of Recorded Daughters in the Sampling Programme:						
	100	200	500	1000	2000	5000	10,000
10	7.0	8.4	9.8	10.4	10.7	11.0	11.0
15	9.8	12.2	14.7	16.0	16.8	17.4	17.5
20	10.8	13.7	17.1	19.0	20.2	21.0	21.3
25	11.2	14.4	18.5	20.8	22.4	23.0	24.0
30	11.3	14.7	19.3	22.0	24.0	25.4	26.0
35	11.3	14.8	19.7	22.9	25.1	26.9	27.5
40	11.2	14.8	20.0	23.4	26.0	28.0	28.8
45	11.1	14.8	20.1	23.9	26.7	29.0	29.9
50	11.0	14.7	20.2	24.2	27.3	29.8	30.8

On the basis of these estimates the NYABC now is concentrating its sire selection almost entirely on a sampling programme.

Selecting Sires for Sampling.

Genetic progress in addition to that accomplished by sampling can be attained in the initial selection of sires for sampling. The Cornell workers have been concerned, as have many others, with methods of selection based on pedigree and on natural service progeny tests. Our experience with the latter has been rather disappointing, but we hope by further research in progress to find some way to improve the prediction of A.I. progeny from the natural service test. Even if this is successful, however, bulls selected on their natural service progeny are very old by the time the A.I. test results are available. Consequently our major efforts in recent years have been dircted toward methods for appraising young bulls. Almost from the beginning of the New York A.I. programme young sires have been used alongside naturally proven bulls. The young bulls were selected mostly on the basis of their naturally sired paternal half sisters and their dams' family records with probably rather more emphasis on distant relatives than we would now recommend. Of most interest is the fact that the young bulls have done just as well as those selected on natural service progeny. The following table taken from Henderson (1954) illustrates this point.

	Number of Bulls	Adjusted Daughter Average lbs. Butterfat
Holstein		
Proven	53	427
Young	20	431
Guernsey		
Proven	12	402
Young	6	432
Jersey		
Proven	5	399
Young	2	402

On the basis of these results NYABC now restricts its sampling to young bulls, the assumption being that they will be at least as good as bulls selected by natural service tests and perhaps considerably better if the selection is concentrated on sons of bulls already proved best in A.I. We wished therefore to learn how best to appraise young bulls for their potential merit as A.I. sires. Combining the principles of the selection index method with our estimates of different causes of variation in records it was concluded that not much improvement in the ranking of young bulls can be made over the relatively simple index which estimates the deviation of these bulls' A.I. progeny from the A.I. breed average by the following weighting factors.

$\frac{1}{2} \quad \frac{n}{n + 12}(s - b)$

$\frac{1}{4}\, h_1^2 \; (a - b)$

$\frac{1}{2} \quad \frac{m h_2^2 \, w}{1 + (m - 1) r} \; (c - a)$ for each close female relative in the lower half of the young bull's pedigree.

n = number of A.I. daughters of sire of young bull.
s = adjusted A.I. progeny average of sire of young bull.
b = A.I. breed average.
h_1^2 = between herd heritability.
a = average of herd in which the young bull was bred.
m = number of lactations of female relative of young bull.
h_2^2 = within herd heritability.
r = within herd repeatability.
w = Wright's coefficient of relationship between the young bull and the female relative.
c = average of m lactations on the female relative.

Unfortunately h_1^2 is unknown but probably low. In practice NYABC restricts its selections to herds of above average production and then proceeds to estimate the young bull as though between herd heritability within the group of selected herds is zero. Probably the only female relatives apart from the paternal half sisters (the sire's A.I. progeny) that are worth considering are the dam and her progeny. If the dam is from an A.I. sire, her paternal half sisters can also contribute a little to estimation of the young bull. The value of young sires selected in the above manner can soon be checked as A.I. daughters of such bulls are now completing their first lactations in New York.

Research in Progress.

In addition to aspects of sire selection already discussed two additional projects will soon yield some results. One of these is a more intensive study of the natural service progeny tests of bulls used in A.I. to see if something was overlooked that might have made more accurate the prediction of A.I. performance. We are looking particularly at the records of the natural service daughters and their dams relative to their contemporary herd mates. A second project of importance to the planning of future breeding programmes is an attempt to estimate components of genetic variance, for example, additive, dominance, and several kinds of epistatic variance.

Research Work Needed.

Two important problems need to be investigated as soon as possible in New York, (1) the validity of our present system of age corrections and (2) the magnitude of between herd heritability particularly with regard to how much emphasis should be placed on the production level of the herd in which a young bull is bred. Obviously the greater the emphasis on herd average the less can be selection on the A.I. proof of the sire and maternal grand sire and on the deviation from the herd average of records of other female relatives of the bull under consideration. With regard to age conversion factors Hickman and Henderson (1955) found very large differences among herds in the increase from first to second lactation. This seems to indicate that different age factors should be used for different herds, provided of course that one can classify herds according to some criterion related to rate of maturity. We hope to investigate this problem in the near future.

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Discussion

Mr. STITCHBURY: Most of our bulls are naturally proven. What were some of the important factors which made some of the New York proven bulls give such disappointing results?

Dr. HENDERSON: We do not know for certain. The records of each bull's daughters were scrutinised carefully and visits were made to the farm before any bulls were purchased in order to detect any unusual circumstances that might affect the records. In spite of this, the natural service proof was not at all closely correlated with the A.I. proof. Differential rates of grain feeding and differences in rates of maturity as influenced by environment are two plausible explanations. We are continuing to investigate natural service proofs in an effort to find some way to make them more reliable predictors of production of the bull's A.I. daughters.

Mr. BRUMBY: From what Dr. Henderson has stated, there appears to be little difference in rate of maturity between daughters of different sires. but large differences between herds. What are some of the factors responsible for these differences?

Dr. HENDERSON: Dr. Hickman and I interpret the former as indicating that rate of maturity has low heritability. If this is so, then the large differences among herds with respect to increase in production from first to second lactation must be largely environmental. We hope by further investigations of these herd differences to find criteria by which we can classify herds according to this increase. If we are successful, we might then recommend age factors that are different from herd to herd.

Dr. CARTER: Would Dr. Henderson tell us what other factors, such as milking ability and productive efficiency, are considered by Cornell workers?

Dr. HENDERSON: In addition to butterfat production used for illustration in this paper, we emphasise in particular milk production. Also we are collecting the following data on daughters of A.I. sires: Various type observations, rate of milking, incidence of ketosis and mastitis, temperament, feeding habits and size. We will not know how much to emphasise these factors as compared to milk production until we have adequate data to estimate their heritabilities and their genetic and phenotypic correlations with milk production.

Professor McLEAN: Have Dr. Henderson and his group considered the need for mating close relatives to these bulls to see if there are any signs of defective recessive genes?

Dr. HENDERSON: Yes, we have given this matter much consideration and have concluded that for the present we shall not carry out a planned test mating programme. None of our approximately 200 bulls thus far used in A.I. have produced progeny demonstrating the presence of serious deleterious recessive genes. If ever we do have trouble of this kind, we shall probably start a test mating programme.

Mr. LAMBOURNE: At what age do the daughters normally calve?

Dr. HENDERSON: The average calving age of our Friesians is about 27 months. The smaller breeds calve at a somewhat younger age and the Brown Swiss at an older age.

Mr. CANDY: Dr. Henderson has made reference to the fact that he has found very little difference between the results obtained using bulls selected on pedigree and naturally proven bulls. What method has been used to measure the results obtained by these two methods

Dr. HENDERSON: Our comparison between the two groups has been based on daughter averages adjusted for the production levels of the herds in which the daughters were milked. On this basis, the bulls selected on pedigree were at least as good as those selected on natural proofs. We cannot be sure just how good either of these groups were. The important thing is that they differed little. That has encouraged us to embark on an extensive young sire sampling programme.

Professor CAMPBELL: Has any attempt been made to use grade sires?

Dr. HENDERSON: No, we have not used grade sires and are not very likely to do so in the near future. We already have available purebred bull calves suitable for sampling in larger numbers than we need.

Mr. YEOMAN: Why do cows that calve in the autumn usually produce more than those which calve in the spring?

Dr. HENDERSON: Spring freshened cows in the United States are handicapped by very poor pasture during our hot, dry summers. In contrast, fall freshened cows are fed liberally on hay, silage and grain during the important part of their lactations.

Dr. HAMILTON: In this country the most important problem in the development of artificial breeding has been the supply of naturally proven sires. By setting a "merit" standard which requires that the maturity equivalent of the daughters must be 380lb. of butterfat or more, we merely select sires from a small proportion of the top herds in the country. Sons of merit sires selected for artificial breeding, therefore, must come from herds which are above the breed average. The assumption underlying these requirements is that the production differences between herds are largely genetic and not environmental. By not adopting some other method of selection we are ignoring about 80 per cent. of the potential bulls which might be available for artificial breeding. Would Dr. Henderson like to comment on this?

Dr. HENDERSON: I do not think this question can be answered until we know what is the relationship between the genetic merit of the bull and the mature cow average in the herd where he is surveyed. Knowledge of inter-herd heritability, when and if available, would only partly answer the question. As the A.I. programme expands, a comparison between bulls' A.I. daughters records and their natural service daughter averages and associated mature cow averages should give some clue to the relative importance of daughter average as compared to deviation from expectancy. As I have mentioned, in New York we select our young bulls for sampling from herds with production above the breed average. We do this for two reasons: First, if inter-herd heritability is appreciably large, we take some advantage of herd difference. Second, it is easier to get a young bull sampled in production-tested herds if the production records in his pedigree are reasonably good.