

PROVING DAIRY SIRES AND DAMS¹

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To "prove" a dairy sire is to estimate his breeding value, which is never observable directly, from the observed qualities of his known offspring. Since these qualities are affected by many other things, the offspring indicate the breeding values of their parents only imperfectly. The various errors which can thus creep into the "proof" of a sire or dam can generally be reduced (in varying degrees) by such procedures as correcting for known peculiarities of the environment, increasing the number of offspring, and comparing the offspring with the observed qualities of the other parents or of still other relatives or of their contemporary herd mates. The problem of "proving" is to use each such procedure in a way that the breeding values will be estimated as accurately as is possible with the available information. The papers on proving dairy sires are far too numerous to list completely. Only articles which still seem to be pertinent and a few which, although now obsolete, have been cited widely are listed here.

PRINCIPLES INVOLVED

Although progeny tests in actual practice are always based on several offspring, the way in which various procedures can diminish the errors in the proof can be seen most clearly by considering first how the record of one daughter indicates her sire's breeding value. A simple way to express this is:

$$y = s + b + r \quad (1)$$

where the letters have the following meanings:

- y is the difference between this daughter's record and the breed average;
- s (for sire's transmitting ability) is the amount by which this sire makes the average of his daughters higher or lower than the breed average;
- b (for bias) is the amount by which the daughters of a sire are above or below the breed average because of any circumstances, other than this sire's breeding value, which are alike for all his daughters; and
- r (for random) is the amount by which this one daughter's record was higher or lower than the records of her paternal sisters.

Since y , s , b , and r all indicate deviations from averages, each of these four variables will sum to zero when several sires each with many daughters are considered, and its plus values and minus values will be about equally frequent.

We wish to know s , but only the record (y) can be observed directly. The many things which can make the daughter's record not indicate her sire's breed-

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ing value accurately are divided into b and r because averaging the records of unselected daughters of a sire will reduce the errors which are grouped in r but will not reduce at all the errors which constitute b . Other procedures, such as comparing the daughter's record with that of her dam, will usually (although not necessarily) reduce the errors from b but increase those from r .

The largest part of b comes from environmental conditions which are identical for all daughters of the same sire but vary from one sire to another. Differences among sires in the average breeding value of their mates can also contribute something to b . This b is a constant for all daughters of the same sire but is a variable from sire to sire.

Most of r comes from environmental effects which vary from lactation to lactation for the same cow and differ among contemporary herd mates. This is shown by the intraherd repeatability of lactation fat or milk records generally being around 0.4 to 0.5. But r also contains any environmental effects which are permanent for a daughter through her lifetime but vary among the daughters of the same sire. An injury causing permanent damage to the udder prior to first calving is an example. Also, r contains the differences caused by the sampling nature of inheritance, whereby some daughters receive one gene and some receive the other from each pair of genes heterozygous in a parent.

Differences caused by dominance, or by epistasis, or by interactions between heredity and environment are largely in r but can be partly in b . Dominance and epistatic differences result from genes having effects when in some combinations which they do not have when in other combinations. Interaction between heredity and environment occurs when the same genetic difference causes a larger phenotypic difference under one environment than under another environment.

Differences in breeding values of the sire's mates and differences caused by the dominance deviations would be wholly in r if the mates of each sire were a random sample of the breed. Actually the mates of a sire usually will be related to each other a little, several being half sisters and a few related in other ways such as daughter and dam, or full sisters, or aunt and niece. Too, the mates of one bull may have been selected more intensively or toward a different goal than the mates of other bulls. This can put much of the differences between dams and a little of the effects of dominance into b .

A small part of the epistasis is included in b , even if each sire is mated to a random sample of cows, since daughters of a sire tend to receive from him a fraction of the special combinations of non-allelic genes. If his mates are related to each other or if they are selected toward a goal uncommon in that breed, more of the epistasis will go into b , although most of the epistasis will still be in r except under extremely unlikely circumstances, such as each bull being mated to a different highly inbred line of cows.

The effects of interactions between heredity and environment will be partly in b because the daughters of a sire will not include the full range of genotypes possible in a whole breed and they usually will not be exposed to the full range

of environments prevailing in the whole breed. Therefore, the interaction effects on paternal sisters will be correlated at least a little.

BIASES FROM SELECTING DAUGHTERS OR MATES OR RECORDS

Daughters. To use only the "best" daughters selects those daughters for whom the r elements happened to be more favorable than average. That large biases are introduced by selecting the daughters is shown by the following figures² for a bull whose 15 daughters have one record each, with the standard deviation among the records of paternal sisters being 80 lb. of fat. The average of the n daughters with the largest records will be above the average of all 15 by about the following amounts:

n	<i>Bias (in lb.)</i>
14	10
12	26
10	41
8	57
5	83

Approximate allowance for the average bias caused by omitting daughters with low records could be made by using these figures, but the actual bias would vary from sire to sire.

The ideal that the daughters shall be absolutely unselected cannot be achieved completely. Natural selection, such as the death of daughters bearing lethal genes or the failure of hereditarily barren daughters to freshen (68), can have affected the data, but probably such things are moderately rare. The herdsman may have culled a few runty or unthrifty heifers before they had a chance to freshen. A heifer may have freshened but produced so poorly that she was discarded within 2 or 3 months and the facts about her may never appear in the proof. Whether selection of daughters was intense can be guessed if the number of daughters in the proof can be compared with the number known to have been born and to have lived long enough that they should have records. Such information is usually difficult to get. More complete reporting and use of records of incomplete lactations would reduce substantially this bias from selecting daughters.

Mates. Selection of the sire's mates (the dams of the daughters in the proof) will generally have been more intense than selection of the daughters, but it introduces much less bias (44). The difference is that the records on which the daughters were selected are in the daughter average, whereas only half of the genic superiority achieved in the mates by their selection appears in the daughter average. When mates' records are subtracted from the daughters' records, as

²Based on Table 20 of the statistical tables by Fisher and Yates. The distribution of butterfat records is near enough to "normal" that this table gives a close approximation to the actual biases.

in a sire index, selection among the mates will have more complex effects since the average records of those cows which survive the selection and appear as dams will be higher than their transmitting abilities. However, subtracting the mates' records will go far toward correcting the usually large errors in b from herd-to-herd differences in environment, if mates and daughters were kept in the same herd and managed alike.

Records. To use only the highest record of the cow is to seek out that record made in the best environment yet experienced by that cow but without knowing what that environment was (10, 13, 24). To use this highest record to predict what the cow or her relatives will do in the future is to predict implicitly that they will continue to get an environment better than average by the same unknown amount: That this bias is large can be seen from the following figures which show the average bias when the standard deviation among records of the same cow is about 60 lb. of fat.

<i>Intensity of selection</i>	<i>Amount of bias in pounds</i>
Highest record out of two	34
Highest record out of three	51
Highest record out of four	62
Highest record out of five	70
Highest two out of three	26
Highest two out of four	40
Highest two out of five	50
Highest three out of four	21
Highest three out of five	33
Highest four out of five	17

An individual buyer might use such figures as these to discount selected records which are quoted to him, but in such small samples as two to five records, this discount could be much too small in some individual cases and much too large in others.

Using the best record is especially unfair for comparing individual cows which do not have the same number of records (8). Suppose three cows actually have the same real ability, but one of them has only one record, one has two records, and one has five records, and the intra-cow standard deviation is 60 lb. Then, on the average, using only the best record of each will make the cow with five records appear 70 lb. better as a producer than the cow with only one record, and 36 lb. better than the cow with two records.

Unfairness from using selected records is generally less extreme for comparing sire proofs than for comparing cows since a daughter average involves several cows and the average number of records per cow for such groups will not vary widely from sire to sire. Selecting the best record will generally bias the average of the sire's mates more than it will bias the average of his daughters because the daughters will be younger when the proof is assembled and will not yet have had as many chances to make high records.

“Abnormal” records. In principle, a record should be discarded when it was made under circumstances likely to have affected the record so strongly and unpredictably that this record is almost useless for predicting the cow's transmitting ability or her producing ability in another lactation. Discarding should be based only on clearly recognizable and specific circumstances other than the size of the record. To use the size of the record itself to indicate when circumstances were “abnormal” enough that the record should be discarded would open the door to most of the biases which come from selecting only the high records for use. An owner or herdsman might, for his own guidance, make some allowance for a cow having had some illness, such as milk fever or mastitis, but it is impossible to be sure how much allowance to make in any such case. It is easy to deceive oneself unknowingly by looking for excuses to discard whenever the record is low but by failing to look for the same circumstances if the record is high. In any event, it is not practical for officials of breed associations or public agencies to make such allowances when proving sires or dams.

WAYS OF MAKING SIRE PROOF MORE ACCURATE

1. *Standardizing environment* can reduce the error. Genes or breeding values are known only by their phenotypic expressions, and these can be modified by the kind of environment which prevails. The very same genotype which would cause a cow to produce 400 lb. in one environment might make her produce 500 lb. in some other environment and only 350 lb. in yet a third environment. Any numerical measurements or definitions of producing or transmitting ability must (whether explicitly stated or not) assume some level or set of environmental conditions as the standard ones under which that numerical value will occur.

If it were physically and financially possible to control the environmental conditions so closely that for every cow in every lactation the conditions actually were standard; or if those conditions were not controlled physically but could be corrected perfectly for the effects of all differences between the actual conditions and the standard ones, then all of the records of a cow would be identical. One lactation record would tell as much about her as any other or as the average of all her lactations. When such a record was used as a proof of her sire, the only sources of error would be Mendelian segregation, the breeding value of her dam, and the vagaries of dominance and epistasis.

Perfect control of the environment or perfect correction for the effects of such environmental variations as did occur is impossible, but since environmental sources are usually responsible for much more than half of the variance in single records of milk and fat (36), any inexpensive physical control or statistical correction which actually does reduce this variation considerably is likely to be worth while. It might be imagined that diligent efforts to standardize the actual environments could make variations in them unimportantly small, but no one has ever demonstrated, by achieving high repeatability of individual records over several years, that this actually can be done, even if the expense of such physical control could be ignored. Standardizing the length of lactation and

correcting for differences in age and in frequency of milking are generally agreed to be worth while, but there is little agreement on the wisdom of making other corrections (15). Likewise, there is little evidence on how much actually could be achieved by attempting to standardize physically the environment of whole herds more than is generally done in D.H.I.A. or H.I.R. herds.

Individuals studying sire proofs often find it profitable to visit the herds and study the barn books or otherwise reach some opinion about the average kinds of environment under which the records were made. Grades or scores for feeding practices or for other environmental factors have been correlated moderately with production in some cases (4, 51), but these studies have not yet resulted in procedures by which a breed association or D.H.I.A. official could correct sire proof more nearly to what it would have been under standard environmental conditions.

The question of what kind of environment should be used as the standard one is still debated occasionally. Common sense indicates that cows should be kept and tested under the kind of environment under which they and their descendants are to be used commercially, but the practical importance of following this guiding principle depends on whether interactions between heredity and environment are large and frequent. The facts yet reported, such as the general sameness of repeatability and heritability at different levels of production (36), agree best with the idea that environmental regimes which cause higher production generally multiply both the environmentally caused and the genetically caused differences between herd mates at somewhere near the same rates. This makes the differences between herd mates larger in absolute units when the production level is high but relatively little more or less reliable for purposes of selection between them. The importance of interactions between heredity and environment is one of the least explored questions in dairy breeding.

2. *Increasing the number of daughters* from one to four reduces sharply the error from r , which is the major source of error when n is small (8, 36, 51). This, of course, raises the accuracy of the daughter average as an indicator of the sire's breeding value. But increasing n does nothing to decrease the errors from b which, if they are at all large, become the main source of error remaining after n is much larger than 3 or 4. Therefore, increasing n above 4 may make only small increases in accuracy. The formula which shows this increase in accuracy with increasing n is that the correlation between y_n and s is:

$$\frac{S}{S + B + R/n} \quad (2)$$

where the capital letters indicate the respective individual variance components caused by s , b , and r . Contrast the situation in which the ratio, $S:B:R$, is 1:5:14 (which might well occur in actual data where the sires were proved in different herds and correction for environmental differences between herds was made only by subtracting the average of the sire's mates as is done in the "equal-parent" or "regression" indexes) with that in which the bias is first removed to make this ratio 1:0:14. The correlation between the sire's breeding

value and the average production of his n daughters then goes up with n as follows:

n	<i>Bias present</i>	<i>Bias absent</i>
1	0.22	0.26
2	0.28	0.35
3	0.31	0.42
4	0.32	0.47
10	0.37	0.65
20	0.39	0.77
00	0.41	1.00

The presence of this bias makes little difference in the accuracy when there is only one daughter but does prevent the accuracy from rising rapidly with n , especially after n passes 3 or 4. If the bias were first removed, raising n from 1 to 4 would nearly double the accuracy but would still leave it far below the limit it could reach. If no bias from b exists and all of the errors are in r , considerable accuracy can be gained by increasing the number of daughters even past 10 or 20. In practice, where at least a few errors from b remain, little accuracy is gained by increasing n past 10 (39).

Many studies of the number of daughters required to prove a sire have really asked of the data only the correlation between the average of the records of the first n daughters and the average of m other daughters (17, 23). In effect, this is asking the repeatability of the daughter average rather than its real accuracy as an indicator of the transmitting ability of the sire. This repeatability, the correlation between y_n and y_m , is simply:

$$\frac{S + B}{S + B + R/n} \quad (3)$$

when n and m are equal. It includes the biased errors in the accuracy. If they are important, this procedure makes the daughter average seem far more accurate for sire proof than it really is. Occasionally this has been distorted even more by asking how nearly the average of the first n daughters is like the average of the first t daughters when the t includes the n (14), or asking how much the proof changes when n increases to t . This contains so much automaticity that the

correlation would be $\sqrt{\frac{n}{t}}$, even if the first daughters of a bull indicated nothing at all about what his future daughters would do.

When bulls are proved in artificial breeding associations (57, 58, 59), b is also reduced with increases in n , since the major portion of b comes from things which differ from one herd to another. Yet, such parts of b as are caused by conditions which prevail over the whole region in which a sire is used artificially, but not over other regions from which come the data on other sires, would not be reduced. For example, New York, Iowa, and Oregon may differ noticeably in average feeding, management, or climate. If each artificially proved sire had been used within only one of these regions, then the effects of the environmental

differences between regions would not be diminished by making n large but would remain in b to mislead one who supposed that the differences between the daughter averages of these bulls were due wholly to qualities of the bulls themselves.

Setting a definite number of daughters as the minimum for proving a sire is arbitrary but must be done if an official scheme is to operate simply and be widely understood. Accuracy is not the only consideration. If the proving is to be much help in breed improvement, many more bulls should be proved than will actually be needed for use after the proof is known. Otherwise one cannot choose for further use only the bulls with the very highest proofs. The proof should be available for action while the bull is still alive and healthy. An important argument for setting the official number as low as five is that thus one can prove more bulls and prove them younger than if more daughters were required. The lower accuracy in the proof on five (which will be only a little lower if b was important) may be more than offset by the opportunity to select more intensively and earlier. Requiring too many daughters could lower the net rate of progress. For example, if 10 bulls are needed and 500 daughters could be used to prove the promising ones, one could prove 20 bulls with 25 daughters each, 50 bulls with 10 daughters each, or 100 bulls with 5 daughters each. The first would be more accurate proof for each bull, but when the results were in, the apparently best half of all bulls tested would have to be used; whereas in the middle case only the apparently best $1/5$, and in the last case only the apparently best $1/10$, would be needed. Under most conditions the extra intensity of selection possible in the middle case would more than offset its lower accuracy as compared with the first case, but the still higher intensity in the third case might not be enough to offset its lower accuracy.

3. *Records of the sires' mates* can be used to correct for differences in the average breeding values of the mates of various bulls and also for such environmental effects as are alike for the mates and daughters of a sire but differ from one sire to another. If the mates of each sire were truly a random sample of the breed and if b were zero, proof by n daughter-dam pairs would be as accurate as proof by $n + 1$ daughters from untested dams (41). Actually the mates are rarely a wholly random sample and b often is large; hence, use of the mates' records is generally more helpful than this.

Use of the mates' records does not invariably lead to more accuracy. If a bull's mates were tested under environment distinctly different from the average environment under which his daughters were tested, use of the mates' records could actually introduce bigger errors than it would remove. Doubtless that happens in some individual cases, but if the environmental effects on mates are correlated with those on their daughters more closely than 0.25, subtracting the mates' average from the daughters' average will make the error less than it would be if the mates' records were not used. That using the mates' records generally corrects the proof enough to be worth while is not conceded by all (17, 26, 42, 56, 59).

To use only the daughters who are out of tested dams wastes the evidence

which is in the records of daughters whose dams were never tested. Most of this information can be had by assuming that the untested dams would have averaged the same as the tested ones, or the same as the contemporary average of the herd in which the daughters were tested.

Since the daughter average is generally about halfway³ between the breed average and the average of the mates (56), the optimum use of the mates' records is to give them only about half as much weight negatively as is given positively to the records of the daughters. This is accomplished merely by adding the daughter-dam difference to the daughters' average to form the "intermediate" or "equal parent" or "modified Mount Hope" index (42). If this intermediate index is then coded by adding half of it to half of the average production of the breed, it becomes Rice's "regression" index. This coding leaves the accuracy of the index for comparing the sires exactly the same but reduces the scale of variation by putting any two sires just half as far apart on the "regression index" as they were on the "equal parent index."

4. *Using the herd average* to correct for herd-to-herd environmental differences has been advocated (34, 50, 59) but has not become used widely. The method presents several difficulties, both in principle and in practice, such as how the herd average should be computed, what cows should be considered contemporary, and what weight should be given to the herd average (49). Measuring a cow's ability by the difference between her records and the herd average is an attempt to correct for differences in environment from herd to herd and (where only her contemporaries are used in the herd average with which each cow is compared) for differences in environment from year to year. Much the same thing as comparing the daughters with their dams is done except that the latter tends to correct also for differences between the average breeding values of the mates of various sires, is based on smaller numbers (49), and is more vulnerable to environmental changes from year to year since daughter and dam usually make their records in different years.

To rate a cow entirely by the difference between her own production and the average of her contemporary herd mates is to assume implicitly that all herds average alike genetically. This is too extreme. Differences in environment are likely to be the major cause of differences between herd averages (59), but herds will also differ at least a little in their genetic composition. If one could know what portion is genetic in the differences between herd averages, he could pay the proper average amount of attention to the herd average by considering each herd as a "family" (43, 49).

Where management varies little between neighboring farms but the environment varies much from one locality to another, a group of similarly managed herds in the same locality might be treated as a single herd (34). The practice

³ That the correlation between mates' average and daughters' average actually is close to the convenient one-half is more of a coincidence than a fundamental biological law. This correlation contains something from genic similarities between daughter and dam but much more from the general tendency of daughter and dam to be tested in the same herd, i.e., from correlations between the herd environments of daughter and dam (42).

in parts of Switzerland of proving sires by comparing the production of their daughters with the average production of all cows in the same testing association (20) is such an effort to correct automatically for local differences in climate, altitude, quality of pasture, etc.

Recently the Milk Marketing Board in Britain (18) has undertaken to prove bulls by comparing the daughters with their contemporaries in the same herd, plus an allowance for differences between herd averages which implies that the causes of differences between herd averages within breeds are one-fifth genetic and four-fifths environmental. In each herd the difference between the average of the sire's n_1 daughters and their n_2 contemporaries is given a weight of $\frac{n_1 n_2}{n_1 + n_2}$ in combining the differences from various herds into a single figure for that sire (59).

At present the commonest policies concerning the herd average are to omit it entirely or merely to list it and let the observer make what use of it he will.

5. *The records of brothers and sisters* contain some information about an animal's breeding value. These records are not ordinarily included in any formal program for "proving" sires or dams. They are really a progeny test of the animal's sire or dam and are only a "sib test" of the animal itself. The common advice to use the son of a proved sire, if a proved sire himself cannot be had, is simply advice to use a bull whose paternal sisters are unusually good.

The sib test is less accurate than progeny test based on the same numbers and under the same conditions, although it is usually more than half as accurate. The sib test is less accurate because chance in Mendelian segregation will permit an individual animal to be considerably better or worse than is typical of its parents' breeding values. Thus, predicting an animal from its sibs cannot be expected to be perfectly accurate, even in the impossibly extreme case in which its sib test is so perfect that its parents' breeding values are known exactly.

The sib test usually becomes available about two years before any daughter completes a record. The sib test is often the best basis, other than the records of his dam and grandams, for making any decisions about a bull during the two or more years before he becomes proved. Decisions which must be made still earlier, such as those before he even has any sisters tested, may have to be based largely on sib tests of his parents, i.e., on the progeny tests of his grandparents. Something like 75% of all bulls born will be first, second, or third calves of their dams. Few of these will have even one maternal sister with a complete record before they are 2 years old. Most of them should begin to have paternal sisters with completed records by the time they are 3 years old if they were born in herds which test regularly. A few which were born when their sires were already old may have fairly complete paternal sib tests even when they are born.

Only a small fraction of the purebred bulls born can ever be progeny tested, since as many bulls as heifers are born and the proving of one bull requires mating him to at least 15 or 20 cows for 1 year. Hence, it is important to choose as accurately as possible which of the young bulls are to be proved.

Accuracy would be maximum if a sire's "proof" included his sibs' records

and all other pertinent information, each item weighted according to its usefulness in that combination. That becomes a selection index which varies with the kinds and amount of information present and can easily become too complicated to include in a formal program for proving sires. The construction and validity of selection indexes are outside the scope of this paper (28, 29, 36). Some simple approximation to a selection index seems useful for proving dams and might include attention to their sibs. An old bull can have so many daughters who tell so much about him that information about his ancestors and collateral relatives would increase only slightly the accuracy of an appraisal of his breeding value, but a young bull or a cow cannot have enough daughters to make this information about sibs and parents unimportant.

6. *Own phenotype* indicates an animal's breeding value distinctly better than one offspring would because chance at Mendelian segregation and the uncertainty about the kind of inheritance received from the other parent do not intervene to dilute the relation between an individual's phenotype and its own breeding value, as they dilute the relation between its breeding value and the phenotype of an offspring. Under most circumstances, more than four offspring are required before the progeny test becomes a more accurate indicator of breeding value than own performance (41), but the number depends on heritability of the character, the amount and kind of prior selection, and the correlation between the offspring for reasons other than that they have this one parent in common. If the character is sex-limited, as milk and fat production are, own phenotype is, of course, not available to help in proving animals of the sex which cannot express the character. A simple way to use own performance in proving dams is to include it in the progeny average with a weight of about three; that is, to proceed as if the cow has three more offspring than she actually does and as if these three all had the same production as this cow does. Three is an approximation to the correct weighting which will vary with heritability and with other circumstances but can hardly ever be less than 2.5 and might even exceed 5. Similar use of own phenotype for bulls may be worth considering when proving for type those who have only a few daughters.

7. *Special aspects of proving dams* which differ from those of proving sires hinge around these differences: (a) a dam can have only a few tested daughters and will be at least 7 years old by the time as many as three of them have records, whereas a bull can have many daughters and may be well proven by the time he is 6 years old; (b) a dam can have production records of her own whereas a sire cannot; and (c) the records of the daughters can be compared with the records of their dams for proving a sire, but for proving a dam, the records of her daughters cannot be compared with any actual records of their own sires. Daughters could, however, be compared with their contemporary herd averages in the proving of dams just as well as in the proving of sires.

Current proposals (52) for proving cows envisage using only the cow's own records, the records of her daughters, and the average record of the daughters of each of her proven sons. It is currently proposed not to call a cow "proven" unless she has had at least three tested offspring. Using also the records of the

cow's dam and of the cow's sibs, of which she would usually have several by the time she has tested daughters, would increase the accuracy of the "proof" although perhaps not enough to be worth the extra computations.

OFFICIALLY SPONSORED PROCEDURES FOR PROVING SIRES AND DAMS

The breed associations for a long time have given various designations, such as gold and silver medals, to sires with a minimum number of daughters attaining a certain level of production in the official testing systems. In a limited sense this might be called a method of proving sires, but the selection of the data introduces so much uncertainty that such designations really tell little except that the sire did have more than the usual number of daughters who produced more than the usual amount.

Current practices in computing "proof" are diverse. In some plans only the daughter average is used with no reference to the production of their dams. In that case, the minimum number of daughters required is usually ten. In plans which emphasize the difference between daughters and dams, the production of daughters out of untested dams may be stated also. Sometimes the records of daughters and dams are merely presented for the breeder to use or interpret as he will. If they are combined into an index, the most common practices are to use the excess of daughters over dams or to add that to the daughter's average (equal-parent or intermediate index), or to average this index with the breed average (Rice's "regression index") so as to reduce the variation of the index. No breed associations have yet incorporated a sliding scale for expressing in the proof the extra confidence which comes with larger numbers of daughters, although that feature is included in Britain in the Milk Marketing Board's "relative genetic values" (18). One common step in this direction is to quote preliminary or "pre-proof" when the number of daughters is still small (usually 5 to 9 inclusive) and to require a larger number (usually at least 10) for definitely recognized proof (3, 62, 63).

In Denmark the cattle breeding societies in 1945 established special stations for progeny testing the sires which are used widely in artificial breeding (26). Between 14 and 20 of the oldest daughters of the bull are leased for a year and brought to the testing stations September 1, just before their first calving. There they are fed and milked under standardized conditions for an average of about 10 months. Each station tests the daughters of two or three bulls at a time. The aims of these testing stations are to reduce the environmentally caused variations, to shift the biased effects to random ones, and to have enough daughters that little error from the random sources remains in the averages. Dams' records are not used because rarely do more than two heifers come from the same farm and the heifers will be from a nearly random sample of dams in that district. This plan has already aroused keen interest in breeding and management practices, but whether it will improve the accuracy of sire selections enough to be worth the expense and effort remains to be seen.

Several associations in the United States have plans for using sire proof in

pedigrees in order to call attention to the young bulls whose sires, dams, and grandparents have unusually good proof and which are, therefore, presumably the best risks for trying as sires (3). The most comprehensive is the Jersey "Star Bull Plan" in which stars are awarded to a young bull when the merit of his relatives is above established requirements (2). This is a kind of selection index in which the bull is estimated farther and farther above the average of the breed as more and better information about him is available. Stars are not taken away from a bull when the information indicates him to be poorer than the breed standards. This feature keeps the plan from publicizing the bulls which presumably should be culled, but it is an incentive to test since the owner does not risk getting harmful publicity.

The association in Friesland in the Netherlands recognizes bulls as "Preferente Stieren" when they and their progeny meet certain standards (55). A graphic daughter-dam comparison is shown for each such bull. For percentage fat he is also assigned a Mendelian formula which postulates four pairs of genes with nearly equal effects. It serves as a sire index having a range of nine classes and it gives a hint about uniformity of the progeny (32).

In Switzerland (20) the Brown Swiss records may be corrected for altitude and for hours the cows worked at draft. Since the herds are small and many bulls are used cooperatively, the records of the bull's daughters are compared with the average of the local testing association rather than with the average of their own dams.

In New Zealand the Dairy Board issues "Sire Surveys" which compare the records of the bull's daughters with the mature cow average of the same herd in the same year (62). The mature cow average is first converted into an "expectancy" figure which is the average of all daughters in herds in which the dams produced at the same level as these dams. Then the bull is considered proven good or bad according to how much his daughters are above or below the expectancy figure for dams with that average. A sire survey is "preliminary" when at least ten of the bull's daughters have one lactation, becomes "intermediate" when eight of these daughters have completed a second lactation, and is "final" when at least six of these daughters have completed three lactations.

Several have proposed to express each record as a percentage of the herd average, or of the breed average, or of the average of records made at the same age—perhaps a moving average extending over 5 or 10 years—and then to use these percentages as measures of a cow's production or for sire proof (9, 34, 35, 50).

MISCELLANEOUS

Heritability of intraherd differences between single 305-day lactation fat records in HIR or DHIA data seems generally to be of the order of 0.2, although a few estimates have been lower than 0.15 or higher than 0.25 (31, 54). If 0.2 is correct for heritability and the standard deviation is 80 lb., the genic standard deviation would be about 35 lb. About one bull in 40 would be expected to raise by that much or more the production of his daughters out of average cows,

whereas only about one in 500 would raise them by more than 50 lb. Questions about normality of distribution of genic values and about whether the heritability fraction is known correctly should prevent extreme reliance on these figures, but they indicate how the rate of improvement is limited by the amount of genic variation present at a given moment as well as by inaccuracies in estimating which animals do have the highest breeding values. The error in sire proof as now conducted must be large since in many cases a bull's daughters do average more than 50 lb. above their dams. The major reason in most cases is that the environment for daughters was better than that for mates although, of course, sampling errors play some part.

The rate of improvement reasonably possible for milk production in a whole breed has been estimated (54) as about 1% per year under natural service without using progeny tests or sib tests and about 2% per year with the optimum use of those and artificial insemination (58). In either case achieving this much would require devoting all the selection efforts to milk production without diverting any attention to type or other characters. These estimates rest on several imperfectly known parameters, such as heritability, replacement rates, and calving intervals, but they seem at least roughly accurate.

Inbreeding has several effects, mostly minor, on the proving of sires and dams. If the sire is inbred, the part played by Mendelian sampling in determining what he will transmit to each offspring is reduced. This shifts part of r into s and thus makes the proof more accurate. If the daughters are inbred, the breeding values of sires and dams are correlated. This also makes the proof more accurate. For example, proving a non-inbred bull by his daughters out of his half sisters makes the s about 1.125 times as large as if his daughters had been out of unrelated mates. However, the inbreeding also shifts parts of the dominance and epistasis from r to b .

Inbreeding is especially useful to find whether a sire carries undesirable recessive genes, such as lethals. The most efficient way of testing whether a sire carries a particular recessive gene is to mate him to several cows who are homozygous for the recessive gene. The next most efficient way is to mate him to several known heterozygotes (6, 7). Inbreeding is the next most efficient way, but unlike the other methods, the inbreeding tests for all kinds of recessives at once whether they are suspected or not. If the sire really is a carrier, about one-eighth of his calves out of his own daughters are expected to be recessives. Among heterozygous sires each tested on n of his own daughters, only $(7/8)^n$ are expected to escape detection. Such reasons led Wriedt (66) to recommend that all dairy bulls thought worth using should be bred as soon as possible to at least 15 of their own daughters in order to learn early whether a sire carried any harmful recessive genes in heterozygous condition. Stopping the further use of the carrier sire and any use of his sons would keep such recessive genes from spreading widely throughout the breed. Wriedt's proposal has not been followed widely anywhere but may meet more approval now that artificial insemination makes it possible to spread the genes of one sire widely. Some allowance for the usual depressing effects of inbreeding on characters such as

milk and fat production should be made when comparing the inbred progeny of one sire with the non-inbred progeny of other sires.

If *specific combining ability* (including both that caused by dominance and that caused by epistasis) is important, a sire's proof on one kind of mates may be distinctly different from his proof on another kind of mates. In that case, the kind of mates chosen for proving him would be important. This would reach its extreme in breeding plans aimed at utilizing overdominance. In general, the sire would be tested on the kind of mates on which he or his descendants are intended to be used.

If dominance of the favorable genes is an important obstacle to accurate selections but there is no overdominance—or if threshold effects of the “margin of safety” kind are important—the proof might be more accurate if extremely low producers were chosen as mates (64). Little is known about whether differences in specific combining ability are important, much less about whether the differences which do exist are caused mainly by dominance, overdominance, or by epistasis. Therefore, little is certain about how much, if anything, could be gained by using special tester stocks for proving sires.

If *interactions between heredity and environment* are important, a different kind of cattle should be bred for each climate, system of management, or ecological niche large enough and different enough from the others to make that worth while. Then it would be especially important that the daughters and their dams be tested under the same conditions as those under which their descendants are intended to be used. The scanty data on the subject make it seem likely that these interactions are small and unimportant when animals belonging to the same breed and used in a moderately uniform region, climate, or system of management are compared. These interactions cannot be neglected so safely when widely different kinds of cattle for world-wide use in a wide variety of climates and systems of management are being compared.

Other characters than milk and fat production could be proved according to the same general principles, but the practical applications may differ widely for reasons such as the following. The character may show at a younger age, as size and much of type do, or at a still older age as longevity and broken udders do. It may show in both sexes, although correction may need to be made for its possibly different expression in males and females. Its heritability may be higher or lower. Environmental effects, such as those from differences between herds, may be more important or less important than they are for milk and fat production. Corrections for such effects may be made more effectively, or less so. The practical importance of the character may be too small to justify much attention, since each bit of attention to other things detracts from the already small amount of freedom to select for important things such as health, milk, and fat production.

Sex-linkage makes a daughter a slightly better indicator of her sire's transmitting ability than she is of her dam's. The effect is as if the sire were completely homozygous for his sex-linked genes while his mates are not. Sex-linkage would also make a bull's maternal relatives better indicators of his breeding

value than his paternal relatives, but it would make a cow's paternal relatives better indicators of her breeding value than her maternal relatives. These differences seem too trivial to be worth attention because only one chromosome pair out of the 30 in cattle carries sex-linked genes. Some have thought it worth attention (46, 60), but the facts they interpreted as suggesting sex-linkage could have resulted from herd-to-herd environmental differences being larger between some kinds of relatives, such as cousins through a paternal grandsire, than between other kinds, such as cousins through a maternal grandsire.

Cow families have received much more mention in the writings on applied animal breeding than their importance justifies (33). So far as the family consists of a cow and her own daughters, this is a case of proving a dam and has real utility. Such proof can be useful in deciding whether the cow's daughters and sons and their offspring are to be used more extensively or less extensively, even when it comes too late for deciding what to do with the cow herself. When the family is extended to include the granddaughters of the cow, the small amount those add to the information about the cow's transmitting ability runs considerable risk of being distorted by environmental changes which have occurred in the longer time interval which has elapsed. Many of the granddaughters are only cousins to each other and through their sires are more closely related to the cows in other "cow families" than to the average member of their own family. Little but self-deception is accomplished by extending the cow family to descendants more remote than granddaughters.

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