THE OPTIMUM EMPHASIS ON DAMS' RECORDS WHEN PROVING DAIRY SIRES*

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INTRODUCTION

Nearly all of the proposals for expressing numerically the transmitting ability of a dairy sire are special forms of the general equation:

$$I = a + c \, (X - bY) \tag{1}$$

Where I = the index or measure used for comparing one sire with another.

   a = a constant which brings the average of the whole group of indexes to the desired level but does not alter the difference between any two sires.

   c = a constant which can be used to expand or contract the variability of I without changing any correlation between it and other variables.

   X = the average record of the daughters of the sire.

   Y = the average record of the dams of those daughters.

   b = a constant which determines the relative emphasis on Y as compared with X.

When only the average of the daughters is used as the proof of a sire, equation (1) becomes: $I = X$; *i.e.*, a and b are each zero while c is 1.0. At the other extreme when the sire proof is considered to be simply the increase or decrease of his daughters over their dams, a is zero but b and c are each 1.0, whence $I = X - Y$. The most widely used sire index (known by various names, such as intermediate, equal-parent, modified Mount Hope, etc.) sets a equal to zero but b to 0.5 and c to 2.0; *i.e.*, $I = 2(X - 0.5Y)$. The recent proposal[1] by V. A. Rice of a "NEW" index is simply to let c = 1.0, b = 0.5, and a = b times the breed average; whence I = 0.5 (breed average) + X − 0.5Y. Turner long ago (page 24 in Missouri Research Bulletin 79 in 1925) proposed to let $I = \frac{100}{85}(X - 0.15Y)$; *i.e.*, a = zero, b = 0.15, and $c = \frac{100}{85}$. These examples show what diverse kinds of indexes are all included as special cases of equation (1).

The real accuracy of an index is measured by its correlation with the true transmitting ability (G) of the sire for which it is computed. The amount of improvement made in the offspring by selecting bulls with equal intensity, but according to I_1, to I_2, . . . or to I_n, is strictly in proportion to r_{GI_1}, r_{GI_2}, . . . or r_{GI_n}. The size of b affects r_{IG} but a and c do not.

The object of the present paper is to show what value of b will make r_{GI} as large as is possible for any index of the type described by equation (1). Also some related problems of using an index are discussed. These ideas

[1] See preceding paper, this issue.

and findings arose largely as a result of discussions with Professor V. A. Rice about his "NEW" index. Helpful suggestions from him and the use of his data for reference are gratefully acknowledged, but he is not to be held responsible for the conclusions or interpretations in the present article.

PREDICTING G FROM Y AND X

Perhaps the simplest derivation of (1) is the ordinary multiple regression equation for predicting G from Y and X. The path coefficient diagram for that, and the pertinent formulas for the best possible prediction of G from X and Y jointly, are shown on the left in figure 1.
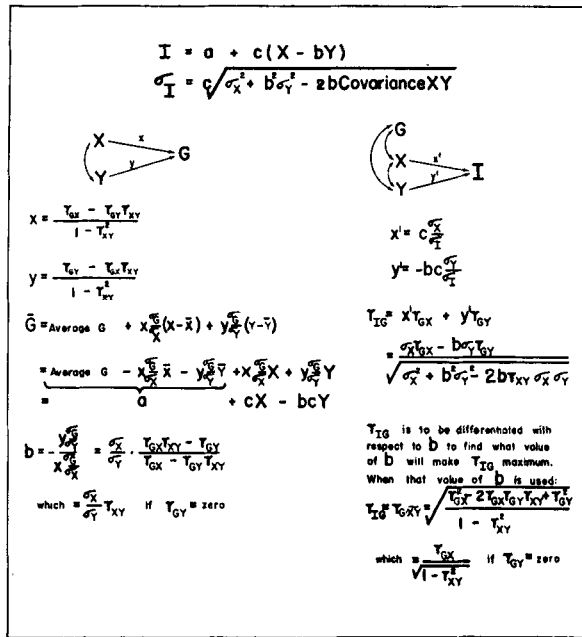

FIG. 1. Biometric relations between daughter average (X), average of mates (Y), and breeding value (G) of sire. Left: Predicting G from X and Y. Right: Correlation between G and any index (I) which is the sum or difference of any multiple of X and any multiple of Y with or without the addition or subtraction of any constant.

If r_{GY} is zero, the formula for b simplifies greatly to: $r_{XY}\dfrac{\sigma_X}{\sigma_Y}$, . . . , i.e., to $\dfrac{\text{Covariance XY}}{\text{Variance Y}}$. That is, the optimum value of b is the regression of X on Y, as Rice maintains. If r_{GY} is a small positive, the optimum value of b will be somewhat less, as is shown more clearly by rewriting the formula for b (figure 1) as follows:

$$b = \frac{\sigma_X}{\sigma_Y}\left[r_{XY} - \frac{r_{GY}(1-r^2_{XY})}{r_{GX} - r_{GY}r_{XY}}\right]$$

The last term within the brackets goes to zero when r_{GY} does but must have

a positive value when r_{GY} does, since r_{GX} is practically certain to be considerably larger than r_{GY}.

The r_{GX} will be positive and of considerable size because each daughter gets half of her G as a sample half of her sire's G. Each daughter's record (O) is partly determined by her own G. Many of the other factors which can make her record large or small will be random from one daughter to another and hence will tend to cancel each other in the average (X) of several daughters. The relation between r_{GX} and r_{GO} is as follows:

$$r_{GX} = r_{GO} \sqrt{\frac{n}{1+(n-1)w}}$$

where there are n daughters and the correlation between the records of paternal sisters is w. In most dairy data collected from many different herds but analyzed as a single population, w is around 0.2 to 0.3, much of this coming from environmental differences between herds, although w also includes r^2_{GO}. Hence in most data used for proving dairy sires r_{GX} will be something like 1.5 to 2.0 times as large as r_{GO}. Reasonable values for r_{GO} (approximately half the square root of the heritability of differences between individual cows) in most dairy data are around 0.2 to 0.3 for quantity of milk or fat and around 0.3 to 0.4 for test.

For r_{GY} to have a positive value requires that there be a general tendency for the breeders who already have high producing cows to try harder than average, and for the breeders who have cows with low records not to try as hard, to get good bulls to mate with them. Further, such a difference in efforts would produce a positive r_{GY} only to the extent that the breeders estimate correctly the breeding values of the bulls at the time of choosing. Presumably there is some difference of this kind in the efforts made but this gives r_{GY} only a very small positive value because the correlation between the real transmitting ability of an untried young bull and the purchaser's estimate of that from the bull's pedigree, or from other information available when the bull is first put to work, is generally small. We shall not be far wrong if we proceed on the assumption that r_{GX} is much larger than r_{GY} although the latter may not be quite as low as zero.

How a positive correlation between G and Y could lower the proper value of b is readily understandable when one reflects that if those breeders whose herd averages are already high do generally succeed in buying young bulls with better-than-average breeding value, then a man seeking to find the best young bulls will have some degree of success if he does nothing but choose the bulls being used in herds which already had better-than-average production at the time those bulls were introduced. This is the line of thought we follow when we sometimes infer that a young bull bought for use in a high-producing herd is probably an exceptionally good bull or he would not have been selected for use in that herd. (Of course we are often wrong in such an inference, but there may well be a gambler's margin in favor of

it.)   Under such conditions Y becomes a positive indicator of G in its own
right and not merely a negative indicator, useful for discounting the effects
of environmental differences from herd to herd and the effects which genetic
differences between groups of mates have on the records of their daughters,
which is its usefulness when r_{GY} is zero.

MAXIMIZING THE CORRELATION BETWEEN I AND G

The optimum value of b can also be found, by setting up the equation for
r_{GI} as indicated on the right side of figure 1, differentiating it with respect
to b, and then finding what value of b will make that differential equal to
zero.   That value of b turns out to be the same as is shown on the left side of
figure 1, as of course it should be.   The two ways of finding the optimum
value of b are the same in principle.

ACTUAL VALUES FOUND FOR b

The values found by Rice for the regression of X on Y for milk in seven
sets of data ranged only from 0.49 to 0.70 with an unweighted average of
0.60.   For fat test the same sets of data yielded values ranging from 0.45 to
0.69 with an average of 0.55.   Using 0.5 for b in dairy data will be nearly
correct, especially if r_{GY} has some small positive value.   On page 33 of the
report of the New Zealand Dairy Board for 1943 a table of expectations for
fat production indicates that the regression of X on Y (the proper value of
b if r_{GY} is zero) in those data is about 0.58 to 0.62.   This table is based on
20,150 daughter-dam pairs which were used in proving 1395 sires.   Paren-
thetically it may be noted that, since the observed regressions are a little
larger than 0.5, the daughter-dam difference seems just a shade more accu-
rate as a sire index than the daughter average alone.

GAIN FROM CONSIDERING THE RECORDS OF THE MATES

The amount of improvement made in the next generation by selecting on
the basis of I is $\dfrac{r_{GI}}{r_{GX}}$ times the improvement to be made by selecting (with the
same intensity) for X alone.   If r_{GY} is zero, this factor reduces to $\dfrac{1}{\sqrt{1 - r^2_{XY}}}$
which in Rice's data has values ranging from 1.14 to 1.27, with an un-
weighted average of 1.21 for milk, and from 1.12 to 1.26 with an unweighted
average of 1.18 for test.   Making some rough allowance for r_{GY} having a
small positive value and for the fact that in actual practice the value used
for b will not always be the exact optimum value for that particular set of
data, the use of I would make improvement from sire selection something
like 12 to 20 per cent faster than if X were used alone.   Thus the gain from
using properly the records of the mates along with the records of the
daughters when proving a sire is not extremely large in dairy data, although
it certainly is real.

It is sometimes argued that the gain from including the mates is not enough to balance the loss from excluding those daughters which are out of untested dams. For this to be true would require that there be few daughters out of tested dams, that there be many out of untested dams, and that the correlation between the records of daughters of the same bull be low. If this latter correlation is as low as 0.24 and bulls are selected on the records of their daughters alone, progress will be 11 per cent faster when they have ten daughters than when they have five; if the correlation between daughters is + 0.30, the corresponding gain will be 9 per cent instead of 11, while with a correlation of + 0.36 it will be increased only 7 per cent, and with a correlation of + 0.42 it will be increased only 6 per cent. The abovè correlations are about what exist between paternal sisters in various aspects of Rice's data on Ayrshires and Holsteins. Therefore the loss from omitting entirely the daughters from untested cows would rarely equal the gain to be had by considering Y properly, even if that required omitting half the daughters. Moreover, where the record of a mate is missing, one could substitute almost as well in the index the average of the other mates or (better still) the average of that daughter's contemporary herd mates who are not by the same sire. With the spread of herd testing, as contrasted with testing only selected individuals, the proportion of daughters who are out of untested dams becomes ever smaller, more of the mates having been tested themselves as daughters in the proving of some earlier sire.

It thus appears that almost the only cost of getting the extra 12 to 20 per cent of progress to be had by including the records of the mates is the clerical cost of assembling and computing their records.

CAUSES OF THE CORRELATION BETWEEN X AND Y

The correlation between the records of individual daughter and dam has generally been reported as of the order of + 0.3 to + 0.4 in most studies of data collected from many different farms but analyzed as a single population. Why such a correlation will usually be different from the r_{XY} which describes the data as they actually are *grouped* in the proving of sires is explained as follows. Figure 2 shows, in terms of path coefficients, how r_{XY} is constituted. The letters have the following meanings:

O = the record of a daughter.

D = the record of a mate.

r = the correlation between the record of a daughter and the record of her own dam.

v = the correlation between the record of a daughter and the record of a mate of her sire other than her own dam.

u = the correlation between the records of two mates of the same sire.

w = the correlation between the records of two daughters of the same sire.

In the numerator of r_{XY} (formula shown in figure 2) v occurs n − 1 times as often as r. The denominator starts out as 1.0 when n = 1 but, as n becomes

indefinitely large, this denominator tends toward n times the geometric mean of u and w, $i.e.$, toward $n\sqrt{uw}$. It seems simplest to think of r_{XY} as a complex average consisting roughly of one part r and $n-1$ parts $\dfrac{v}{\sqrt{uw}}$. Most of this shift of r_{XY} from r toward an expression which is mainly dominated by v, u, and w, is usually accomplished by the time n is as large as five. The regression of X on Y is $\dfrac{\sigma_O}{\sigma_D}r$ when $n = 1$ but tends toward $\dfrac{\sigma_O}{\sigma_D} \cdot \dfrac{v}{u}$ as n becomes indefinitely large.
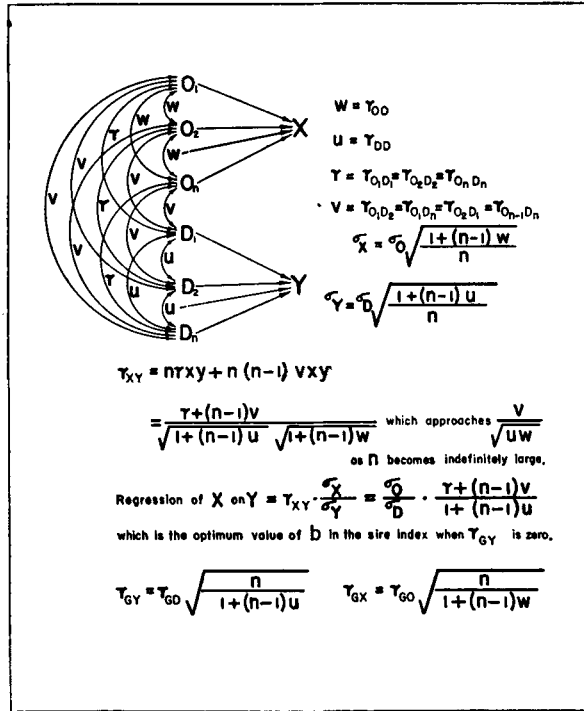

FIG. 2.   Biometric relations between X and Y, showing how r_{XY} is constituted of r, v, u, and w, and may be very different from r.

In proving dairy sires, n has a minimum value of five (in the Dairy Bureau procedure—six, ten, or more in various of the registry association procedures), but is usually variable in any list of proved sires from which r_{XY} may be calculated. That is, sires which have been proved on exactly five daughter-dam pairs will be included in the same list with sires which have been proved on six, seven, or more pairs. Variations in n cause r_{XY} or b or $\sigma_X{}^2$ or $\sigma_Y{}^2$ to shift from one limiting value toward another in proportion to the changes in the reciprocal of n. Therefore, the harmonic mean[2] of n

2 The harmonic mean of n is the n which has a reciprocal equal to the mean of the reciprocals of the actual n's.

should be used when analyzing into their constituent parts (r, v, u, and w) the r_{XY}, b, σ_X or σ_Y computed on a population of proven sires in which n was a variable. The harmonic mean will be less—sometimes considerably less— than the arithmetic mean. For example, the first 220 indexed sires in Volume 14 of the Holstein-Friesian Red Book had n's varying from 6 to 83, although for half of them n was 12 or less. The arithmetic mean was 15.2 while the harmonic mean was 11.2. For the first 152 Holstein proved sires in Misc. Pub. 522 from the U. S. Dept. of Agr. the arithmetic mean was 8.77 but the harmonic mean was 7.60. Here n ranged from five to 35 but half the sires were proved on seven pairs or less. Among the 73 Ayrshire proved sires listed in the same publication, the arithmetic mean was 7.40 and the harmonic mean was 6.88.

In table 1 are shown the values for u, w, and v computed from the data Rice shows in his tables 1 and 4. Because the statistics on X and Y (Rice's

TABLE 1

The ingredients of r_{XY} in V. A. Rice's data on Holsteins and Ayrshires

Statistic	Milk		Test	
	Ayrshire	Holstein	Ayrshire	Holstein
r^1	0.29	0.32	0.48	0.43
v^2	0.26⁵	0.18	0.12	0.18
u^3	0.36⁵	0.28	0.28	0.22
w^4	0.47⁵	0.28	0.28	0.36
2(r − v)	0.06⁶	0.29	0.72	0.51

^{1} As given by Rice.

^{2} Computed from the values of r_{XY} in Rice's table 4, substituting the values given for r in his table 1 and the values computed here for u and w.

^{3} Computed from the formula: $\dfrac{\sigma_Y^2}{\sigma_D^2} = \dfrac{1 + (n-1)u}{n}$.

^{4} Computed from the formula: $\dfrac{\sigma_X^2}{\sigma_O^2} = \dfrac{1 + (n-1)w}{n}$.

^{5} Somewhat inflated because the data in Rice's table 4 include a considerable time trend.

^{6} The correct figure here will be larger than this by about twice the size of the bias mentioned in footnote 5.

table 4) came from a slightly different sample of Herd Improvement Registry data than the statistics on O and D and because in dairy data the standard deviation tends to vary with the mean, Rice's observed $\dfrac{\sigma_Y}{\sigma_D}$ and $\dfrac{\sigma_X}{\sigma_O}$ were multiplied by the ratio of the corresponding means before computing u and w. Even after this correction, the figures for u, w, and v are still inflated (as compared with r which comes wholly from Rice's table 1) wherever the data from Rice's table 4 covered a longer period in which there was a marked time trend. This seems to have been important only for the Ayrshire milk. The data concerning Ayrshires in table 4 were collected over a period of 25 or 30 years, whereas the Holstein data go scarcely half that far

back. For Ayrshire milk the time trend was marked, since the means in Rice's table 1 are 7.1 per cent larger for daughters and 5.8 per cent larger for dams than the corresponding means in his table 4. For Ayrshire test and for the Holstein data the time trend was too small to have much effect on the present analysis, the maximum increase of any of these means in his table 1 over the corresponding mean in his table 4 being only 1.2 per cent. For computing the u, w, and v shown here in table 1, the observed harmonic mean of 11.2 was used for n in the Holstein data and 11.5 was used in the Ayrshire data. (The Ayrshire arithmetic mean actually was 13.39 but the distribution of n was not available for computing the harmonic mean directly.)

Causes of r, u, v, and w

Figure 3 shows how r, u, w, and v are caused partly by differences in breeding value and partly by differences in environment. Environment is used here to include all other causes of variation in the records except differences in the genetic value of the cows which made them.

The meaning of the symbols is as follows:

g^2 is the fraction of the phenotypic variance ($\sigma_O{}^2$ or $\sigma_D{}^2$) due to additively genetic differences between individual cows.

e^2 is the fraction of the phenotypic variance which is not additively genetic.

d is the genetic correlation between mates of a sire. It has a moderate positive value because some of the mates are related to each other and also because some breeders try harder than others to breed and select for high production.

m is the average genetic correlation between the sire and a mate. It will be very little above zero, since most breeders try to avoid even mild inbreeding. Assortive mating on somatic likeness must be indirect since the male cannot exhibit the characteristic himself. Hence assortive mating can contribute but little to m. Moreover assortive mating is not extreme for these characteristics, since no one tries intentionally to mate low producing cows to bulls with unusually low production in their pedigrees.

r_{EE} is the correlation between the non-genetic causes of variation for the individual denoted by the subscripts. It has a moderately large positive value because herds differ much from each other in their management, as well as in uncontrolled environmental conditions such as weather, condition of pastures, etc. Generally r_{EE} will be larger between daughters than between mates, or than between a daughter and a mate, because the daughters' records are more nearly contemporaneous and thus are subject to more nearly the same peculiarities of management and weather or other environment.

r_{GE} exists only to the extent that the herds with the highest intrinsic breeding values are also fed and managed better than the average herd, while herds with low intrinsic breeding values are fed and managed less well than average. There may well be some of this in dairy data but r_{GE} must be small because of the uncertainty concerning the breeding value of the average animal while it is yet alive and because no one intentionally tries to collect and breed low producers. The G and the E in r_{GE} pertain to different individuals.

The environmental terms and the terms for cross-correlations between genetic and environmental causes of variation (figure 3) are almost the same

in r as they are in v, except when a sire is proved in two or more herds. In such cases the environmental term included in r is certain to be larger than the corresponding one in v. Because their other terms are so nearly the same, subtracting v from r leaves a remainder which comes close to equalling $\dfrac{g^2(1-d)}{2}$. Doubling this and then making allowance for d yields an estimate of the heritability of differences between records of mates of the same sire. Figures for $2(r-v)$ are shown in the bottom line of table 1. Dividing these by something like 0.85 to 0.95 (to allow a reasonable amount for d)

Composition of r, u, v, and w.

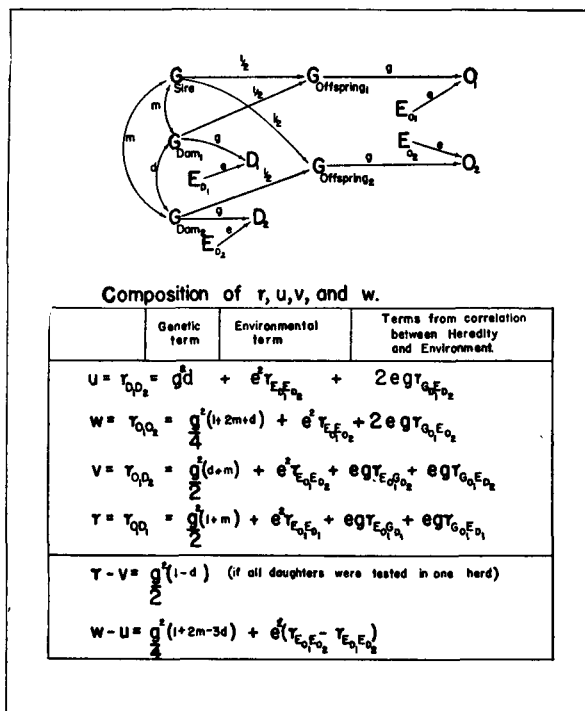|	Genetic term	Environmental term	Terms from correlation between Heredity and Environment
$u = r_{D_2 P_2} = $	$g^2 d$	$+ \; e^2 r_{E_{d_1} E_{o_2}}$	$+ \quad 2eg \, r_{G_{d_1} E_{o_2}}$
$w = r_{O_1 O_2} = $	$\dfrac{g^2}{4}(1+2m+d)$	$+ \; e^2 r_{E_{o_1} E_{o_2}}$	$+ 2e \, g \, r_{G_{o_1} E_{o_2}}$
$v = r_{O_2 P_2} = $	$\dfrac{g^2}{2}(d+m)$	$+ \; e^2 r_{E_{d_1} E_{o_2}}$	$+ eg \, r_{E_{d_1} G_{o_2}} + eg \, r_{G_{o_2} E_{d_1}}$
$r = r_{O_1 O_1} = $	$\dfrac{g^2}{2}(1+m)$	$+ \; e^2 r_{E_{o_2} E_{o_1}}$	$+ eg \, r_{E_{d_1} G_{o_1}} + eg \, r_{G_{o_1} E_{d_1}}$
$r-v = $	$\dfrac{g^2}{2}(1-d)$	(if all daughters were tested in one herd)	
$w-u = $	$\dfrac{g^2}{4}(1+2m-3d)$	$+ \; e^2 \left(r_{E_{o_1} E_{o_2}} - r_{E_{o_1} E_{o_2}} \right)$	

FIG. 3. Path coefficient diagram showing the causes of the correlations between the records of daughters and of dams.

yields estimate of heritability of intra-breed differences between cows. A small amount should then be deducted from that to allow for the (comparatively few) cases in which a sire was proved in two or more herds differing (of course) somewhat in management. The estimate of milk in the Ayrshire breed is certainly too low because of the time trend which contributed considerably more to u, w, and v than it did to r,[3] as was mentioned above. The

[3] The figure for r came wholly from Rice's table 1 which covered only a short period of time. The figures for u, w, and v came from differences or ratios between statistics in his table 1 and in his table 4, the latter having extended over a considerably longer period.

three other estimates are compatible with most of those derived from other studies, namely something under 0.3 (perhaps under. 0.2) for differences in milk records and something of the order of 0.5 to 0.7 (or less if the data included many sires which each had daughters in more than one herd) for differences in test. A strong influence of contemporaneity on Ayrshire milk and Holstein test may be indicated by w being so distinctly larger than u, but perhaps that needs confirmation on more extensive data before effort is spent on finding an explanation for it. Certainly the daughters' records would generally have been made within a more restricted range of time than the records of the dams.

The similarity of r_{XY} in the data for Herd Improvement Registry (Rice's table 4) and in the Dairy Bureau data for Dairy Herd Improvement Associations (Rice's tables 2 and 3) tempts one to suppose that heritability and the other factors affecting sire proving are the same in both kinds of data. However, the numerical value of r_{XY} depends more on the ratio of v to u and w than it does on the difference between r and v. The topic merits further study.

OPTIMUM VARIABILITY FOR SIRE INDEXES

The variability of a sire index does not alter its *accuracy* (provided there are at least 16 to 20 classes from the lowest to the highest figure) but may affect considerably its convenience in use and its susceptibility to misinterpretation. The variability of the index can be made as large or as small as one chooses by altering the value of c. Two plausible definitions for the variability which a sire index should have for maximum convenience in actual use are as follows: A. The index should equal the most probable breeding value of the sire. B. The index should have the same standard deviation as the records of cows.

The theoretical advantages of standard A are obvious. It expresses the sire proof directly in terms of the goal for which indexes (and indeed all forms of progeny testing or estimating breeding value) are intended. Under it the c of equation (1) should make $\sigma_I = r_{GI}\sigma_G$. To do this requires that c be approximately $\dfrac{g^2}{2} \cdot \dfrac{\sigma_0^2}{\sigma_x^2} \cdot \dfrac{1}{1-r^2_{XY}}$ which in the data pertaining to dairy sires comes close to $2g^2$. For example, it has values of 1.65, 1.82, 2.10, and 1.84 g^2 in Rice's table 6 for Ayrshire milk and test and Holstein milk and test, respectively. Unfortunately the value of g^2 is not known with high certainty (*i.e.*, within really narrow fiducial limits) in any population. In most dairy data it seems to be around 0.15 to 0.30 for quantity of milk and somewhat higher—perhaps above 0.50—for test. Moreover g^2 will vary a bit as there is more or less care in controlling or correcting for environmental variables, a larger or smaller number of daughters, whether single records or lifetime averages are used for daughters and for dams, etc.

Attempting to state the proper numerical value for c turns the spotlight

on the practical difficulty of using standard A, namely the uncertainty about the precise value of g^2 to use, the variation (usually slight) in that from one population to another, and the large variation in g^2 from one characteristic to another, with the resultant necessity of using one formula for test, another for milk, etc. Also many will think "most probable breeding value" is more theoretical and intangible than an actual record (D or O) which is a familiar and very real thing to them. If standard A is used, the index of a sire cannot be compared directly with the record of a cow until the cow's record is first translated to the scale of "probable breeding values" by regressing it $1 - g^2$ of the way toward the breed average.

Any change from one standard to another will always cause considerable confusion. It would be unfortunate to adopt standard A now and start indexing sires, using 0.40 as c for milk and 0.80 as c for test, only to find three or four years later that 0.50 and 1.10 or 0.30 and 0.70 would have been more accurate for most dairy populations. Eventually we may come to standard A or something very similar, but the change should first receive considerable scrutiny and much trial and actual practice.

Standard A automatically discounts the records for the average amount of non-genetic variation in them and thus protects the user against too easily falling a victim to his wishful thinking. No index can be guaranteed to show the breeding values of each individual proven sire correctly but a scale which is just as likely to rate an individual too low as too high is less susceptible to misinterpretation than one on which the high indexes are generally higher and the low indexes are generally lower than the breeding values of the sires to which they apply.

Standard B puts the indexes of sires and the records of dams on an equal footing, so that they can be compared directly.[4] For c_I to equal c_D exactly

4 Strictly speaking, this requires that mean I and mean D be approximately equal

(since in most dairy data X differs little from Y) and that $\dfrac{\sigma_I}{r_{IG}} = \dfrac{\sigma_D}{r_{DGd}}$ where Gd is the breeding value of the cow who has record D. The writer has shown (JOUR. DAIRY SCI., 18: 1–19. 1935) that r_{IG} and r_{IGd} will not be far apart if heritability is larger than 0.10 and especially if (as seems almost always to be the case in dairy data collected from several herds) the environmental contribution to the correlation between daughters of a sire is $+0.10$ or larger. The argument may be reviewed here in slightly different terms by referring to the composition of r_{IG} as shown in figure 1. When $r_{GY} = $ zero and $r_{XY} = 0.5$,

r_{IG} reduces to $r_{GO} \sqrt{\dfrac{n}{1+(n-1)u}} \sqrt{\dfrac{4}{3}}$. Now r_{GO} is half the correlation between a daughter's record and her own breeding value. This latter correlation will be the same as between a dam's record and her breeding value (r_{DGd}), except as more intense selection among the dams than among the daughters may have reduced r_{DGd} slightly and more lactations per dam than per daughter may have raised r_{DGd}. Hence $\dfrac{r_{IG}}{r_{DGd}}$ is approximately $\dfrac{\sigma_O}{\sigma_X} \cdot \dfrac{1}{\sqrt{3}}$ which isn't very far from unity. It has values ranging from 0.86 to 0.99 in Rice's table 6 but perhaps should be increased a little to allow for the dams having been a bit more highly selected than the daughters were. In short, selection of dams on their own records will rarely be either much less or much more accurate than selection of sires on their indexes.

requires that $c = \dfrac{\sigma_D}{\sqrt{\sigma_X{}^2 + b^2\sigma_Y{}^2 - 2br_{XY}\sigma_X\sigma_Y}}$. If r_{GY} is zero and $r_{XY} = 0.5$, this

is $\sqrt{\dfrac{4}{3}}\ \sqrt{\dfrac{n}{1 + (n-1)w}}$ which, for most of the likely values of n and w, gives

c a value not far from 2.0—more often a little less than a little more. Rice's table 6 would require for c values of 1.74, 1.71, 2.03, and 1.85, respectively, to make the index conform exactly to standard B. The EP index, now rather widely used, has 2.0 for c and therefore comes fairly close to standard B. The EP index cannot be equalled for simplicity of computation, among indexes which use an approximately correct value for b.

If the index is used only for comparing the sires with each other and with cows, no further step than standard B is necessary. For reducing indexes (or records of cows) to breeding values or for predicting the production of future offspring the indexes (or records) need to be regressed toward the average of the breed far enough $(1 - g^2$ of the way) to allow for the average amount of non-genetic variance in them. If this second step is neglected or not understood, the user of indexes constructed according to standard B (or the user of cows' records) may easily build hopes too high (in terms of actual pounds or per cent) on the bulls or cows with the high figures and may damn more severely than he should those with low figures.

In principle standards A and B differ only in that the regression toward the breed average is "built into" the operation of figuring the index under A and hence is already accomplished when the index is obtained, while B requires two steps to reach the same goal. The first step yields the index itself, which can be compared directly with the records of cows but is more variable than breeding values. The second step (which is not necessary for comparing sires with each other or with cows and hence is often omitted) is to estimate probable breeding value from the index by regressing it $1 - g^2$ of the way toward the breed average.

Rice's NEW index, which uses 1.0 for c, comes near to standard A for test but the proper value for c for quantity of milk is not that large. The breeding values of sires for amount of milk or of fat will generally be nearer to the breed average than their NEW indexes. The NEW indexes are simply EP indexes regressed half way toward the breed average—i.e., the NEW index for each bull is exactly half way between his EP index and whatever constant figure is used for the breed average in computing the NEW index. Since this difference is only one of coding (i.e., the EP index is divided by two and then has a constant added to it to form the NEW index), the two indexes have the same correlation with any other variable and are equally accurate for comparing one sire with another.

PREDICTING THE ACTUAL PRODUCTION OF FUTURE DAUGHTERS

For predicting the production of a future daughter the correct procedure in principle is simply to average the most probable breeding values of the dam

and the sire. Then this average should be raised or lowered enough to allow for the environment in which the daughter is to make her record being better or worse than average. But in practice we rarely have any direct measure of that environment. Probably the average record of that herd for the most recent two or three years could be used advantageously for this purpose, but this is not yet being done generally. The environment pertaining to the daughter will usually be correlated slightly (something of the order of $+0.2$ to $+0.3$) with the record of her dam if she and her dam make their records in the same herd. It will usually be still more closely correlated (something of the order of $+0.4$ to $+0.6$) with the index of her sire if she is to make her record in the same herd as the one in which her older sisters made the records on which that index is based. In this latter case the sire index assumes a large part of the predictive value which would attach to the direct measure of the daughter's herd environment if such a measure were available. Because of its lower correlation with the herd environment, the dam's record does not assume much of this predictive value for environment if the sire index was made in the same herd but it does assume considerable if the daughter is to make her record in the same herd as her dam but in a different herd from that in which her sire was proved. If the daughter is to make her record in a herd in which neither her dam nor her sire's earlier daughters were tested (an uncommon case in dairy data), then both the sire's index and the dam's records are useful only for their genetic relation and neither of them will help as an indicator of the herd environment under which the daughter will make her record.

If sire indexes are to be used almost solely for estimating the production of future daughters, either singly or in groups, then one can make a good case for building into the index enough extra variation to allow also for its importance as an indicator of non-genetic circumstances (*i.e.*, for the kind of environment) which will prevail for that daughter or those daughters. But D also should receive extra weight for its real, although generally lesser, usefulness for the same thing. This leads at once to four different scales for c_I and c_D (or four different factors by which to multiply them), according to whether the future daughter is to make her record in the same herd as her dam and her older paternal sisters, in the same herd as her dam but a different one from her sisters, in a different herd from her dam but the same herd as her sisters, or in a different herd from either her dam or her sisters. Possibly there is some simple way of doing that but it seems to the writer probable that the simplest way will be to use standard A (which is standard B regressed $1-g^2$ of the way toward the breed average) and then modify the prediction up or down according to whether the most recent average of the herd in which the daughters are to be tested is above or below the breed average.

Predictions of the production of an individual future daughter cannot be expected to be highly accurate. A correlation of around 0.1 to 0.2—*i.e.*,

g^2 times the square root of one-half—between the actual and the predicted record of the individual daughter (for quantity of fat or milk—a bit higher for test) is about as much as can reasonably be expected if the dam has only one lactation and the sire's proof was of only average accuracy and the daughter is to make her record in a different herd. Although this would be raised distinctly if the dam is judged by all of her records and if there were three or more of those, and if the sire's proof is unusually accurate by reason of a large number of daughters and unusually careful discounting of the environmental circumstances which applied to his daughters and mates, yet it seems unduly optimistic to expect by that means to attain an average accuracy as high as a correlation of $+0.4$ between actual record and predicted record.

The average production of n future daughters can of course be predicted more accurately than the production of one daughter. This is only an automatic result of the averaging process and does not introduce any new biological principle. The averaging permits many of the chance circumstances, which cause a daughter to produce more or less than was predicted, to cancel each other's effects in the average of n daughters. The correlation between prediction and fact is $\sqrt{\dfrac{n}{1+(n-1)w}}$ times as large when predicting the average production of n daughters as when predicting the production of one daughter. Also σ_X is only $\sqrt{\dfrac{1+(n-1)w}{n}}$ as large as σ_0 and this of itself makes the error of prediction seem smaller, if that error is measured in actual pounds or percent instead of being measured relative to σ_X or σ_0. The net result is that in actual units the standard error of estimating the average of n daughters is only $\sqrt{\dfrac{1-w+n(w-t^2)}{n(1-t^2)}}$ as large as the standard error of estimating one daughter, where t is the correlation between prediction and fact when predicting one daughter.

SUMMARY

Nearly all sire indexes which have been proposed can be described by the general equation, $I = a + c(X - bY)$, in which a, b, and c are constants, X is the average production of the daughters, Y is the average production of their dams and I is the index.

The size of a affects only the general level (the mean) of the indexes. The size of c affects the variability of I but not its accuracy for comparing the breeding values (G) of two or more indexed sires. The size of b affects the acuracy of the index as well as its variability.

The main contribution of this paper is in showing that maximum accuracy of the index is attained when $b = \dfrac{\sigma_X}{\sigma_Y} \cdot \dfrac{r_{GX}r_{XY} - r_{GY}}{r_{GX} - r_{GY}r_{XY}}$. If $r_{GY} = $ zero this

optimum value of b becomes simply the regression of X on Y.   If r_{GY} has a small positive value (as is possible if breeders whose cows have high records generally try harder than other breeders to get good bulls—and if the extra efforts are partially successful) the optimum value of b is a little less than the regression of X on Y.   The regression of X on Y is about 0.5 to 0.6 both for milk and for test in most sets of data actually used for proving dairy sires.   The optimum value for b in dairy data will, therefore, be not far from 0.5.

If r_{GY} is zero, selection of sires on the optimum index, as thus defined, will make $\dfrac{1}{\sqrt{1-r^2_{XY}}}$ times as much progress as choosing the sires on the average of their daughters alone.   The size of this factor, when r_{GY} is very small and r_{XY} has such values as are usually encountered in proving dairy sires, is about 1.12 to 1.20.

The size of r_{XY} or of the regression of X on Y is affected more by the correlation (v) between a daughter's record and the record of a mate of her sire, other than her own dam, than it is by the correlation (r) between a daughter and her own dam, especially when n is large.   The regression of X on Y approaches $\dfrac{v}{u}$ and r_{XY} approaches $\dfrac{v}{\sqrt{uw}}$ as a limit when n becomes extremely large, u being the phenotypic correlation between the mates of the same sire and w being the phenotypic correlation between daughters of a sire.

A sire index can be made as variable as desired by adjusting c.   The value 2.0, used for c in the intermediate or equal-parent indexes makes σ_I generally just a little larger than σ_D or σ_O.   This index can be used rather fairly for comparing proven sires directly with individual cows, as is necessary in evaluating pedigrees.   It is, however, more variable than real breeding values.   Consequently, if it is to be used directly as the sire's most probable breeding value, the index needs first to be regressed far toward the breed average (just as cows' records do) to allow for the average amount of non-genetic variation in such indexes.   Approximately this amount of regression would already be accomplished in an index which used for c twice the heritability of differences between the records of individual cows.   Rice's proposed "NEW" index, which uses 1.0 for c, is the equal-parent index regressed half way toward the breed average.   It is, therefore, half as variable but has exactly the same accuracy.