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Mate Selection by Selection Index Theory*

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Summary Mate selection by selection index prediction of total merit in expected progeny is proposed as a rational basis for making recommendations in the choice of a bull to which a cow may be mated. Growth in USA of service programs recommending bulls to particular cows has motivated the need to rationalize mate selection processes. This paper illustrates that mate selection on the basis of highest index value for expected progeny among potential mates can justify special mate selection programs, when a nonlinear relationship exists between at least one trait in the index and merit.

Key words: Selection index – Mate selection – Economic values

Introduction

Selecting one of a number of bulls to mate a particular cow differs from selection of a bull for general mating in a cow population. The criteria to choose bulls for artificial insemination (A.I.) usually do not depend on the particular genes of potential mates. The principle of selecting on a bull's general combining ability or breeding value under random mating is the usual basis for developing selection methods.

An alternative principle of selecting one bull instead of another for mating a particular cow may depend on the attributes of the cow or class of cows being mated.

During the last decade in the USA, a significant rise in the number of cows mated where a consultant (in A.I. organization or private) chooses a bull mate on the basis of attributes and records on each cow. About 1.5 million dollars is spent annually for services to select a mate for about 9 million cows (Halsey 1978). The consequences of these mate selection practices remain undocumented. The specific practice of selecting mates for a cow is commonly referred to as 'corrective mating.'

The purpose of this paper is to show that mate selection may be described as a multi-trait selection method depending on the traits of the first preselected mate of a mating pair. A formulation of mate selection into the selection index theory, familiar to professional animal breeding researchers, will encourage further study and increase the resolution of investigations into the consequences of various mate selection methods.

Net Merit Index for Net Worth of Genotype When all Economic Relations are Linear

A net merit index is an instrument to rank animals on their transmitting values. In principle, the index was defined by Hazel (1943) as the sum of the contributions expected toward net worth of the genotype (i.e. array of additive genetic values), where each contribution toward net worth is specifically related to a differential in the genetic value for each trait. Expressed in terms of the predicted genetic value of each trait (Henderson 1963), net merit index is

$$I = a_1 I_1 + a_2 I_2 + \dots + a_k I_k,$$

where I_i is an index prediction of the genetic value of the i^{th} trait,

and a_i is the constant economic value contributed toward net worth by each unit difference in the genetic value of i^{th} trait.

The expected progeny genetic value is the midparent value of corresponding genetic values for each trait when

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only additive inheritance of genetic effects is considered. The genetic value of one trait is referred to interchangeably as its breeding value (BV). The prediction of genetic values (I_i) similarly is referred to as the estimated breeding value (EBV_i). Continuing, the net merit index is a prediction of the net worth of the progeny based on the pairs of parental I_i's or EBV_i's. The progeny net merit index is

$$I_p = a_1 \tfrac{1}{2}(I_1^* + I_1') + a_2 \tfrac{1}{2}(I_2^* + I_2') + \ldots + a_k \tfrac{1}{2}(I_k^* + I_k') \quad (1)$$

where I_i^* is an index predicting the genetic value of trait i of the dam, and

I_i' is an analogous prediction for the sire.

The expected progeny net worth can be rearranged so the sire and dam net merit indexes are expressed as separate factors, i.e.

$$I_p = \tfrac{1}{2}(\sum_i a_i I_i^*) + \tfrac{1}{2}(\sum_i a_i I_i')$$

$$= \tfrac{1}{2} I^* + \tfrac{1}{2} I'$$

The factoring of separate non-overlapping sire and dam contributions to the expected progeny net worth indicates that the contribution of each parent is independent of the contribution from the alternate parent. Therefore, selection practice designed to maximize progeny net worth need only focus on selecting the individually superior females or males for breeding. No necessity exists to select particular mating couples to maximize the expected progeny net worth.

Practical Selection Objectives Imply Non-linear Economic Values

Recommendations made by advisory personnel or private consultants while developing a comprehensive breeding program for dairy cattle have categorized traits as having different selection objectives. A non-exhaustive list of categories is:

i) maximize or minimize value for a trait,

ii) maintain trait at level where no benefit is expected from continued change in one direction, while change in alternative direction is undesirable, and

iii) avoid extremes and favor intermediate values for a trait.

These various objectives imply that different relationships occur between the values for a trait and the corresponding contributions to the net merit of the individual. A constant unit economic value over the range for a trait can be described by a straight line relationship and is referred to as a linear relationship. Relationships not restricted to a straight line are referred to as non-linear. Non-linear relationships describe the pattern of changes in economic values over the range of interst for a trait. The general form of an economic relationship implied from each selection objective is illustrated in Figure 1. The traits listed under each objective are examples relevant to dairy cattle breeding.

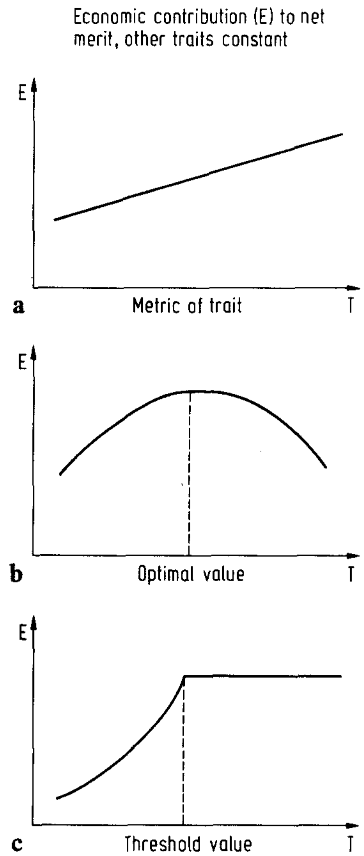

Fig. 1a-c. Illustration of linear and non-linear relationships between economic contribution (E) to net merit and a trait metric (T). **a** Linear relationship: e.g. Traits where maximum is desired1. milk solids yield; 2. udder support; 3. mastitis resistance. **b** Non-linear relationship: e.g. Traits where intermediate is desired 1. udder and teat conformation; 2. set of feet and legs; 3. body size. **c** Non-linear relationship: e.g. Traits where lowest acceptable value is desired 1. ability to reproduce and function (move, eat, ...); 2. calving ease or milking ease; 3. minimal level of disease (milk fever, edema, ...)

The independent selection of potential mates is applicable where unit economic values are constant. A more realistic definition of net merit including non-linear economic values leads to a mate selection method depending on the evaluation of each potential mating pair as a couple (Wilton and Van Vleck 1969).

Example of Mate Selection When an Intermediate Value for One Trait is Desired

Figure 2 shows a hypothetical, but realistic, relationship that might be expected between scores for straightness of rear legs and the relative economic returns expected from

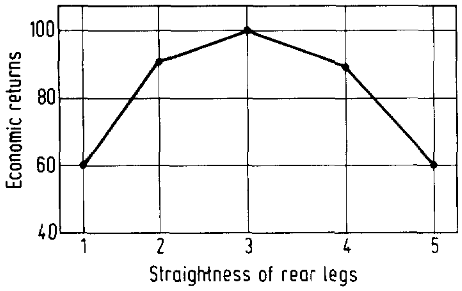

Fig. 2. Hypothetical relationship between economic returns and score for straightness of rear leg. Scores denote: extreme sickleness = 1 to very straight = 5

individual cows. An intermediate score for straightness has the highest relative returns. Increasing or decreasing degree of straightness from the intermediate score becomes associated with adverse effects on mobility of the cow leading to an increase in health care or shortened herdlife.

Any mate selection method which chooses mates to maximize the net worth of progeny will select a mate for a cow depending on her estimated breeding value (EBV) for straightness of rear legs. Table 1 shows how the EBV of a cow affects the choice of a mate when maximizing returns in progeny from the example trait. The mean progeny BV is expected to be the arithmetic average of the two parent BV's, when the contributions from each parent is additive. The choice of the best mate to achieve an intermediate BV in progeny requires a choice in EBV which when averaged with alternate parent's produces an expected progeny BV closest to the BV having maximum returns. In this example, the best paired values were ($EBV_♀$, $EBV_♂$) = (1,5), (2,4), (3,3), (4,2), (5,1). The special pairing is required because differences in the genetic basis of leg scores are not proportional to differences in the return expected, i.e. non-linear.

Table 1. Returns in progeny according to EBV of mated pair, using relationship in Figure 2

	EBV of Cow				
EBV of Bull	1	2	3	4	5
1	60	78	90	98	100
2	78	90	98	100	98
3	90	98	100	98	90
4	98	100	98	90	78
5	100	98	90	78	60

Net Merit Index for Net Worth of Genotypes When Some Economic Relations to Trait Scores are Non-Linear

Essentially, the net merit index, predicts the net worth of a genotype by summing the predicted economic contribution from each trait. The net merit index may be written, in terms of the economic contribution from the genetic value of each trait, as

$$I = e_1\{I_1\} + e_2\{I_2\} + \ldots + e_k\{I_k\}.$$

Each element, $e_i\{I_i\}$, is a possibly non-linear expression in I_i. The non-linear expression may in addition be defined in terms of other traits I_k ($k \neq i$) (Wilton et al. 1968). Formulating an expected net worth of progeny from parental EBV's for the simplest case, the net merit index for progeny becomes

$$I_p = e_1\{½(I_1^* + I_1')\} + e_2\{½(I_2^* + I_2')\} + \ldots + \\ + e_k\{½(I_k^* + I_k')\} \quad (2)$$

The net merit index for expected progeny is simply the substitution of the expected progeny BV for an individual EBV on a trait by trait basis.

Expression (2), in contrast to expression (1), can not be factored into components involving only separate parental contributions. This means mating to achieve maximum levels in progeny net worth will be achieved only by evaluating the net merit index for each potential sire and dam pair. Choices on individual sire or dam net merit indexes separately will not in general lead to best mate selection. Choice of the best mating pair requires that a matrix of progeny net merit values be defined and examined. A matrix of net merit values for expected progeny may be defined such that sires are organized row-wise and dams organized column-wise. This setup is illustrated in Table 2. Analogously, the effect of herd means, representing cows as dams was discussed (Van Vleck 1971). The best mate for each dam would be determined by selecting the maximum value index in a column and identifying the sire responsible for the highest index. In practice, selection in dairy cattle would occur in two stages. First select the females for breeding, then select the particular male which maximizes net worth among a dam's possible progeny.

Table 2. Illustration of expected progeny net merit indexes according to sire and dam coordinates

	Dams				
Sires	D_1	D_2	D_3	....	D_m
S_1	I_{11}	I_{12}	I_{13}	....	I_{1m}
S_2	I_{21}	I_{22}	I_{23}	....	I_{2m}
.	.	.	.		
.	.	.	.		
.	.	.	.		
S_n	I_{n1}	I_{n2}	I_{n3}	....	I_{nm}

Mate selection Illustrated for Three Hypothetical Traits, Two Having a Non-Linear Relationship with Economic Contribution to the Net Worth

The example considered uses three traits each likely to represent the broad categories of traits referred to above, and here defined, respectively, as a production trait, a maintenance trait, and a trait with an intermediate optimum. The production trait has a constant economic value for each additional unit of production, the maintenance trait must be at some minimal level without incurring relative large costs, yet levels above a threshold value have no additional benefit. The intermediate trait is similar to the illustration in Figure 2. Figure 3 shows the relationship for each of the three traits used in the example.

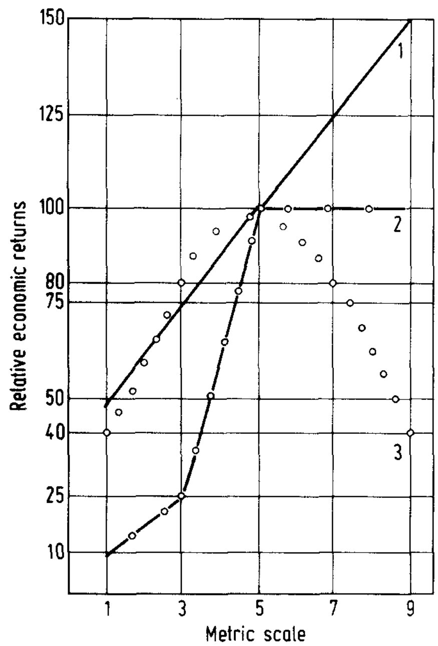

Fig. 3. Relationships of the relative economic contribution to net worth of individuals and the genetic value of each of three hypothetical traits: 1 = production, 2 = maintenance, 3 = intermediate

Mate selection is considered for a particular female having EBV's for each of the three traits. Note the EBV for a trait is the index prediction (I) for that trait. Three potential sires for her progeny are under consideration. The indexes for the three traits (i.e. EBV's) and their corresponding economic values are given in Table 3. Ignoring the level of the traits of the cow, bulls are ranked on their individual net merit index as: B over A and B over C.

Table 3. Index prediction of breeding values and economic contribution to net merit index for a cow and three potential mates[a]

			Bulls					
Trait	Cow		A		B		C	
	I	e{I}	I	e{I}	I	e{I}	I	e{I}
Production	5	100	7	125	9	150	5	100
Maintenance	3	25	3	25	3	25	9	100
Intermediate	3	80	5	100	7	80	1	40
Net merit index		205		250		255		240

[a] Bulls are ranked on the net merit index B>A>C

Evaluation of the net merit of expected progeny from each possible mating using expression (2) is given in Table 4. The rank of the mated pairs was (Cow, Bull C) over (Cow, Bull B) over (Cow, Bull A). The interaction of EBV's of the bulls with the EBV's of the cow is evident, since the bulls rank differently depending on whether only individual merit is considered or whether joint merit with the cow traits is considered. The ranking of mating pairs on expected progeny merit takes into consideration the complimentary nature of alternative bull and cow EBV's according to the economic benefits expected along

Table 4. Net merit of expected progeny from each possible mating[a]

	Progeny of					
	(Cow, Bull A)		(Cow, Bull B)		(Cow, Bull C)	
Traits	I	e{I}	I	e{I}	I	e{I}
Production	6	113	7	125	5	100
Maintenance	3	25	3	25	6	100
Intermediate	4	90	5	100	2	60
Net merit index		228		250		260

Index value of each trait is arithmetic average of parental values.
Additive gene action is assumed
[a] Progeny of mated pairs are ranked on net merit index as (Cow, Bull C) > (Cow, Bull B) > (Cow, Bull A)

the scale of measurement of each trait. Table 5 shows the difference of the expected progeny minus the dam in each trait's contribution to net merit. The complimentary effects of the EBV's of a bull and the EBV's of the cow become evident. More total gain occurs from the maintenance trait overcoming some loss in the intermediate trait in the progeny of bull C than modest gains expected in the production and intermediate traits for the other bulls as sires.

Table 5. Difference of expected progeny minus their dam for each trait contribution to net merit

	Progeny minus Dam		
Trait	Sire A	Sire B	Sire C
Production	+13	+25	0
Maintenance	0	0	+75
Intermediate	+10	+20	−20
Net merit	+23	+45	+55

In effect the most economically deficient characteristic of the cow was met by mating with bull C, contributing to greatest gains in progeny net merit. The high maintenance trait score of bull C complimented well with the low score of the cow. The economic value of a unit increase in the maintenance trait above the cow's EBV was greater than any possible change in other traits. The economic value of one unit increase in score for each trait above the cow's EBV were +13 for the production trait, +38 for the maintenance trait, and +10 for the intermediate trait. Any potential mate with significant superiority in a trait which compliments well with the particular array of economic values implied from the EBV's of the cow leads to gains in progeny merit. Bull C provided the greatest level of superiority for this cow's array of EBV's without also having any significant losses in the expected progeny net merit from Bull C's EBV's for the remaining traits in progeny net merit.

Mate Selection by Index Theory

Selection of a mate for each pre-selected cow may be viewed as a second stage in the process of defining pairs of mates (Allaire 1977). The first stage would be the initial choosing of cows as dams of future replacements. This is a practical reality in cattle breeding. In a general overview, the choice of mating pairs be visualized as illustrated in Table 2. Whenever one mate is restricted to one mating per breeding season, the choice of best subset pairs is restricted to a particular column or row of Table 2. In an unrestricted ranking of all pairs from all possible mates some potential mates may be used a number of times depending on the number of select pairs occurring in a particular row or column.

Mate selection formulated from non-linear economic values may be compared to the mate selection which occurs in crossbreeding (Moav 1973). In crossbreeding each member of a mated pair is selected to complete a pair, whose properties are known to produce a heterosis effect among the progeny in one or more traits. In contrast, mate selection using a net merit index ranks pairs on the basis of the unexpected progeny merit using the interacting economic contributions from each mate. As crossbreeding seeks to use a special interaction of parental genotype which contribute in a non-additive way to the genetic merit of progeny, mate selection by index uses the special interaction of parental economic merits of each trait. Essentially, a particular set of economic weights are determined for each animal to be mated depending on its known genetic values. The net merit index of the expected progeny determines the economic interaction of the genetic values of a mated pair. Economic contributions depend only on the function of economic returns relative to the score values for a trait. The interaction of economic merit considered here may occur when transmission of genetic values from parent to progeny is strictly additive.

Economic Improvement Needs a Wide Spectrum of Potential Mates

Mate selection by indexing potential mating pairs highlights the importance that potential mates (e.g. bulls available in artificial insemination) represent a wide spectrum of genetic values for the traits of importance. The extent of the spectrum in EBV's needed over a number of traits, of course, would depend on the variety which exists in the general nature (i.e. linear relations, threshold valued, intermediate valued optimum) of the alternative relationships between economic returns and the biological traits. For example, bull C in Table 3 ranked lowest on individual net merit, but ranked best among three bulls for a particular set of cow EBV's. This occurred not only due to the array of cow EBV's but also due to the three economic relationships included in net merit. Maximum economic improvement can only be made when the best combinations of EBV's exist among potential mates, are recognized by mate selection methods and mated to obtain the expected progeny.

Research Needed on Quantifying the Relationship Between Economic Returns and Various Traits

The hypothetical relationships defined and shown in Figure 3 were required to proceed with the mate selection example. In practice, similar relationships are necessary to formulate a realistic mate selection method. Further research within economically important species should include the possibility of developing a non-linear relationship when estimating regressions of economic returns on the metric of a trait.

Some economic relationship curves can be determined from the deterministic modeling studies. Still other studies need to be conducted defining a metric (or scale) for a trait with a sufficient number of gradients to allow for the possibility that a non-linear economic relationship may be discovered, should one exist.

Conclusions

Mate selection methods may be defined in terms of a selection index where the estimated breeding value of an individual for each trait is replaced by the estimated mean (i.e. estimated breeding value) of progeny from a potential mating pair. Mate selection can be justified, in contrast to individual selection of mates separately, when the economic values of each trait change with each potential mate depending on the magnitude of the expected breeding value of the progeny from the proposed mating. Indexing a potential mating pair, under additive inheritance, evaluates the economic interaction between mates, both within traits and among traits. Future studies in economically important species should allow the possibility that economic value may be non-linear in the metric of a trait of interest.

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