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A note on the effect of variation of lactation length on the efficiency of tropical cattle selection for milk yield

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Summary. The effects of procedures generally used to reduce variation of lactation length on the efficiency of selection for milk yield are examined applying existing theory to a set of average literature estimates of heritabilities and correlations between lactation yield and length. Adjustment of milk yield for lactation length should be expected to remove more genetic than phenotypic variation, thus reducing selection efficiency in relation to unadjusted yield. Selecting individuals on an optimum index of lactation yield and length would be more efficient for improving yield than selecting on yield alone, while both criteria would have practically the same efficiency for selection on progeny test. This result could be applied to reduce milk recording frequency without losing selection accuracy. Culling on lactation length before selecting on yield would have little effect on individual selection efficiency. However, excluding short lactation records should be expected to reduce both selection accuracy of the progeny test and genetic variation in yield.

Key words: Lactation length – Tropical dairy cattle – Dairy cattle selection

Introduction

Short lactations are a major problem of milk production in tropical systems. While in intensive temperate systems lactations shorter than 305 days are mostly terminated by "abnormal" reasons (death, illness or injury), in tropical systems "normal" early drying also occurs. Short lactations have a genetic base: the refusal of zebu and Criollo cows to let milk down in the absence of the calf is well known, but short lactations also occur when the calf stimulus is used. High grade Holstein-Friesian crosses are unable to sustain lactation under poor husbandry conditions, while high grade zebu crosses do not respond to improved management (Madalena et al., in preparation). Within breed genetic variation of lactation length and high genetic correlations with milk yield have been reported (Babona et al. 1982; Barbosa and Pereira 1983; Bodisco and Abreu 1981; De Alba and Kennedy 1985; Gill and Balaine 1971; Ledic et al. 1986; Lobo 1976; Lobo et al. 1980; Lopez and Planas 1982; Meyn and Wilkins 1974; Reis 1983; Schneeberger et al. 1982; Solanki et al. 1973). Thus, simultaneous genetic improvement of lactation length and yield may be desirable in tropical environments, contrary to the situation in intensive temperate conditions where genetic potential for lactation length is not limiting.

Although the importance of lactation length has been recognized for a long time (Rhoad 1935), there is no consensus of opinion on procedures for handling this trait in genetic studies of milk yield. Three basic procedures are commonly found: (a) to adjust milk yield by the phenotypic regression on lactation length; (b) to exclude from the analysis short lactations, considered "abnormal" (typically shorter than 100–150 days); and (c) to use all records available, not eliminating observations nor adjusting yield on the basis of lactation length.

Mahadevan (1966) justified excluding abnormally short lactation records to increase selection accuracy "except where the short lactations are genetic in origin". Briquet (1967) advocated against extending short lactations of genetic origin, such as in zebu type animals. However, lactation length is often times included as a covariable in models for genetic analysis of milk yield. Ngere et al. (1973) extended yield to mean lactation length when records terminated by loss of calf, and excluded observations with other codes associated with premature record termination because no extension factors were available. Records of cows sold, although shorter than normal, were not extended because "terminations were not associated with identifiable environmental disturbances". Kiwuwa et al. (1983) excluded lactations not reaching 75 days as abnormal. A similar approach was followed by DeAlba and Kennedy (1985), who used restrictions on maximum length and yield. Franklin et al. (1976) followed procedure (c) to allow selection for yield to operate against short lactations. Buvanendran (1977) and Madalena et al. (in preparation), among others, utilized procedure (c) for comparisons of crossbred groups.

In comparisons of breeds and crosses, procedures (a) and (b) selectively remove variation between groups in lactation length and associated variation in lactation milk yield. Madalena et al. (1987) presented an example of this situation, where crossbred group effects were attenuated under procedures (a) and (b), resulting in under estimation of heterosis and breed additive difference in relation to procedure (c).

Arguments for expressing yield in a fixed lactation period (Johansson and Rendel 1968) seem valid for within breed animal evaluation, in tropical as well as in temperate systems, although a standard length longer than 305 days might be justified for tropical populations – given their longer calving intervals – to allow better expression of breeding values for lactation length.

In this paper, the consequences of utilizing the above procedures on the efficiency of intra-population selection for milk yield are examined applying well known theoretical results. A set of average genetic and phenotypic parameters are utilized to exemplify likely results in practice.

Symbols and average parameters used

Two cases are considered: individual mass selection, applicable to selection of bull dams, and sire progeny testing. A single record per female is assumed. Define

$Y =$ lactation milk yield (in 305 days or longer fixed period) the trait to be improved by selection. Additive genetic value is denoted by y.

$X =$ lactation length. Both X and Y refer to actual, non-manipulated traits, as in procedure (c). Subscripts a and b will be used to indicate traits in these two procedures. Thus,

$Y_a =$ $Y - b_a X =$ milk yield adjusted by the phenotypic regression of Y on $X(b_a)$.

$R(W) =$ $i_W R_{yW} \sigma_y =$ genetic gain in trait Y by selecting on criterion W, there i_W indicates selection intensity for W, R_{yW} the correlation between y and W, and σ_y the additive genetic standard deviation of yield.

$E(W/Z) = R(W)/R(Z) =$ relative efficiency of selection criteria W and Z to improve Y. In particular,

$E =$ $E(X/Y) = rh_X/h_Y =$ efficiency of indirect mass selection on lactation length relative to direct selection for yield.

h^2_X and h^2_Y indicate the heritabilities of X and Y, and r and R the genetic and phenotypic correlations between them. Averages of literature estimates of these four parameters were utilized to evaluate alternative procedures. Mean values were as follows (number of estimates in parenthesis):

$$h^2_Y = 0.30\ (26),\ h^2_X = 0.27\ (13),\ r = 0.95\ (5),\ R = 0.57\ (13)\,.$$

Estimates of r were consistently very high for several breeds: 1.16 for Gir (Solanki et al. 1973), 0.79 for Hariana (Gill and Balaine 1971), 0.99 for Guzera (Barbosa and Pereira 1983), 0.97 for Pitangueiras (A. M. Lemos, personal communication) and 1.27 for Friesian (Babona et al. 1982). Estimates of $r > 1$ were replaced by the upper limit $r = 1$ for averaging. Other parameter estimates were obtained from the reviews of Lobo (1976) and Reis (1983) and reports of Bodisco and Abreu (1981), DeAlba and Kennedy (1985), Franklin et al. (1976), Ledic et al. (1986), Lobo et al. (1980), Lopez and Planas (1982), Mahadevan (1966), Meyn and Wilkins (1974), Rhefeld (1975) and Schneeberger et al. (1982).

Adjustment for lactation length

Removing variation for lactation length should not necessarily increase accuracy of selection for milk yield. The heritability of adjusted yield is

$$h^2_{Y_a} = h^2_Y(1 - RE)/(1 - R^2)\,,$$

which will be <1 if r and R have equal sign and $E > R$, as is the case with the literature parameters, where $h^2_{Y_a} = 0.72\ h^2_Y$.

Thus, the phenotypic adjustment may reduce heritability by removing more genetic than environmental variation. Heritability should also be expected to decrease due to record selection, which removes some variation in lactation length (Robertson 1977). Experimental examples of these two situations have been reported (Table 1). However, Abubakar et al. (1986) reported that heritability of 305-day yield was relatively unaffected by eliminating short lactations (<60 or <90 days) or by projecting yield to 305 days, although these procedures

Table 1. Heritability estimates for different procedures of reducing variation in lactation length: (a) lactation length adjusted yield; (b) short lactations excluded; (c) all observations, non-adjusted

Trait	Procedure	$h^2 \pm$ s.e.	Reference
Lactation	a	0.08 + 0.03	Reis (1983)
milk yield	c	0.19 +0.04	
305-day	b*	0.44 n.a.	DeAlba and
milk yield	b**	0.28 n.a.	Kennedy (1985)

Criteria for excluding lactations:
* length < 30 days and yield < 100 kg
** length < 150 days and yield < 450 kg

reduced total phenotypic variation of yield, suggesting that in their Jamaica Hope data parameters were different from the literature set. Actually, Schneeberger et al. (1982) reported $h_X^2 = 0.19$, $h_Y^2 = 0.35$ and $R = 0.64$ in the Jamaica Hope. Selection may reduce the incidence of short lactations (Hayman 1974; Reason et al. 1979) and thus decrease the heritability of lactation length and its genetic correlation with yield, which might explain the divergent results in the relatively more improved Jamaica Hope. Cady et al. (1983) reported a marked decrease of heritability of 305-day yield in buffaloes, as a result of eliminating lactations shorter than 250 or 305 days.

The relative efficiency of the phenotypic index for mass selection is

$$E(Y_a/Y) = (1 - RE)/(1 - R^2)^{1/2}, \qquad \text{(Searle 1965).}$$

The latter author showed that $E(Y_a/Y) > 1$ if r and R were of opposite sign, or if $E < 1$ and $R > 2E(1 + E^2)$. This is not the case for the parameter set used here, making Y_a a very inefficient selection criterion (Table 2).

The efficiency of selection based on the progeny test for Y_a, relative to the progeny test on Y, is

$$E(\bar{Y}_a/\bar{Y}) = (1 - RE)/(1 - 2R\,Q_{xy}/Q_y + R^2\,Q_x/Q_y)^{1/2}$$

where $Q_y = 1 + (n-1)\,h_y^2/4$, $Q_x = 1 + (n-1)\,h_x^2/4$, n = number of daughters and $Q_{xy} = R + (n-1)\,E\,h_y^2/4$. The progeny test of Y would be more efficient than the progeny test on Y_a (Table 2).

Experimental evidence of the inadequacy of adjusting yield for lactation length was presented by Franklin (1983), who reported an annual genetic trend for unadjusted lactation milk yield of 0.8% of the mean, while the genetic trend for adjusted yield was about one half of that, "indicating that a significant proportion of the response can be attributed to a genetic improvement in lactation length".

Alternative indexes

For individual selection, maximum improvement would be obtained by selecting on

$$I = Y - b_0 X$$

where the optimum weight is

$$b_0 = (\sigma_Y/\sigma_X)(R - E)/(1 - E\,R) = (b_a - E\,\sigma_Y/\sigma_X)/(1 - E\,R), \qquad \text{Purser (1960).}$$

Since $b_a \neq b_0$, selecting on Y_a will be less effective than selecting on the optimum index, i.e., $E(Y_a/I) < 1$, unless $E = 0$.

The efficiency of the optimum index relative to direct selection on Y is

$$E(I/Y) = [1 + (E - R)^2/(1 - R^2)]^{1/2}, \qquad \text{Searle (1965),}$$

which is always > 1 unless $E = R$, i.e., selecting on an optimum index is always better than or equal to selecting on component traits, as is well known. For the average literature parameter set $I = Y + (\sigma_Y/\sigma_X)\,0.681\,X$, which would be 8% more efficient than direct selection (Table 2). This should justify selecting on I, although in practice some efficiency would be lost because of errors in estimates of parameters to develop the index (Sales and Hill 1976).

Table 2. Relative selection efficiencies of criteria to improve milk yield. Individual selection based on one record, efficiency relative to selection on yield. For progeny testing, efficiency relative to progeny test on yield of n daughters. Results based on $h_Y^2 = 0.30$, $h_X^2 = 0.27$, $r = 0.95$, $R = 0.57$

Criteria	Individual selection	Progeny testing	
		$n = 40$	$n = 80$
Phenotypic index (Y_a)	0.59	0.80	0.85
Optimum index (I)	1.08	1.03	1.01
Lactation length (X)	0.90	0.94	0.94

The optimum index to combine the progeny means $\bar{Y}$ and $\bar{X}$, $I_p = \bar{Y} - (\sigma_Y/\sigma_X)\,b_p\,\bar{X}$, has weight

$$b_p = (Q_{xy} - Q_y\,E)/(Q_x - E\,Q_{xy})$$

The relative efficiency of selecting on I_p instead of on $\bar{Y}$ is given by

$$E(I_p/\bar{Y}) = (1 - b_p\,E)/(1 - 2\,b_p\,Q_{xy}/Q_y + b_p^2\,Q_x/Q_y)^{1/2}$$

For example, for $n = 40$ and $n = 80$ daughters, $b_p = -0.446$ and -0.328, respectively, for the average parameter set. In this case the superiority of the index over $\bar{Y}$ would be negligible (Table 2).

It is interesting to note that selection on lactation length would be an acceptable alternative (Table 2), considering its lower cost of recording. This result is due to the high genetic correlation and similarity of heritabilities of X and Y in the average literature parameters used, and may not hold generally. However, since milk recording cost is a major limitation for the establishment of dairy cattle selection programmes in developing countries, it seems worthwhile to examine the possibility of developing indexes of lactation length and milk yield recorded at longer intervals than the conventional monthly frequency.

Exclusion of short lactations

This case is similar to a two stage selection process: a proportion, $1 - p_1$, of records with $X < L$ is discarded in the initial stage, and then a proportion p_2 of the remaining animals is selected on yield (Y_b). The final proportion selected is $p = p_1 p_2$. Genetic gain may be predicted by

$$R(Y_b) = \sigma_Y [i_X (E - R) + i_{Y_b} (1 - R E)]/(1 - R^2),$$

Young and Weiler (1960),

and this can be compared with gain by selecting on Y only, with selection intensity corresponding to p ($i_Y h_Y \sigma_Y$). Ratios of relative selection efficiencies $E(Y_b/Y)$ are presented in Table 3 for $p = 0.02$ and $p = 0.10$. These values were chosen because only intense selection of bull dams would be of interest in practical programmes. Approximate values of i_X and i_{Y_b} were obtained from Young and Weiler's (1960) chart for $R = 0.5$. It may be seen in Table 3 that record culling would have little effect of the efficiency of individual selection. Thus, the reduction in selection intensity for Y would be compensated by indirect response to selection on X, and only minor benefits would accrue from culling at optimum levels for each trait.

The efficiency of progeny testing selection is altered in three ways by record culling, in relation to procedure (c):

(1) Sire evaluation is based on fewer daughters, $n' = n p_1$.

(2) Genetic variation in yield is reduced to

$$\sigma^2_{y'_b} = \sigma^2_y (1 - r^2 h^2_X k), \qquad \text{Dickerson and Hazel (1944)}$$

where $k = i_X (i_X - t_X)$ and t_X is the standardized value of truncation point L.

(3) Sire differences in lactation length and correlated yield tend to level off, making poor sires appear better than they really are. Thus, $\bar{Y}_b$ would have a lower correlation with y than $\bar{Y}$. This correlation, adapted from Dickerson and Hazel (1944) is

$$R'_{y\bar{Y}_b} = R_{y\bar{Y}} [(1 - r^2 h^2_x h^2_y k/4)/(1 - r^2 h^2_x h^2_y k\, n'/16\, Q'_y)]^{-1/2}$$

where $Q'_y = 1 + (n' - 1) h^2_y/4$.

Table 3. Efficiency of selection for milk yield excluding short lactations relative to selection utilizing all records, based on $h^2_Y = 0.30$, $h^2_X = 0.27$, $r = 0.95$, $R = 0.57$

	Proportion of records excluded				
	0.10	0.20	0.50	0.70	0.80
Individual selection					
Final selected proportion					
0.02	0.97	0.99	1.00	1.02	1.01
0.10	0.97	0.98	1.04	1.02	1.02
Progeny testing					
Progeny no.					
40	0.95	0.91	0.82	0.72	0.64
80	0.96	0.93	0.86	0.78	0.72

Intensity of sire selection will not be affected by record culling, so $E(\bar{Y}_b/\bar{Y}) = R'_{y\bar{Y}_b} \sigma'_{y_b}/R_{y\bar{Y}} \sigma_y$. It may be seen in Table 3 that relative selection efficiency was <1 for the average literature parameter set, the efficiency loss being aggravated by more intense record elimination, as might be expected.

The two stage selection theory assumes bivariate normal distribution of X and Y, which might not be a good approximation for populations with few short lactations.

The question of whether lactations terminated by "abnormal" records should be extended or not (or excluded, in the absence of appropriate extension factors) is not considered here, except by suggesting that it should be answered by comparing expected genetic gains under each alternative course of action. The above formulation provides a logical framework to this end, since it is independent of whether records are considered abnormal or not, although the parameters involved may then change. If no parameters are available, e.g., at the start of a selection programme, two extreme kinds of error may be committed: (1) to extend/eliminate "abnormal"lactations, assuming that cause of abnormality is environmental, which, if untrue, would hide from selection undesirable genetic variation associated with yield; or conversely, (2) not to extend nor eliminate records, considering cause of abnormality to be genetically determined, which, if untrue, would reduce milk yield heritability by increasing environmental variation. Thus, arbitrary decisions not based on experimental information may not be innocuous, unless abnormal records are rare.

Conclusions

(1) Genetic variation in lactation length may be utilized to enhance selection gains for milk yield in tropical cattle by applying standard selection index methods.

(2) Procedures removing variation in lactation length may be expected to reduce efficiency of selection for yield, unless heritability of lactation length and its genetic correlation with yield are low in the population concerned.

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