

IMPLICATIONS FROM DAIRY CATTLE BREEDING EXPERIMENTS

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CHARACTERIZATION OF SELECTION EXPERIMENTS

Several American universities and the federal departments of agriculture in the US and Canada have conducted dairy cattle selection experiments in the last 30 years (White et al., 1977; Young et al., 1977; Blake et al., 1986; McAllister et al., 1990). The experiments in the US were a part of two regional projects with federal funding; NC-2 (Young et al., 1977) and S-49 (White et al., 1977).

The Canadian project is unique in that selection for protein yield (McAllister et al., 1990) and crossbreeding (McAllister et al., 1994) took place simultaneously using foundation populations previously selected for total solids yield (Hickman, 1971).

Only two studies (McAllister et al., 1990; Legates and Myers, 1988) used bulls produced from the selection and control lines to perpetuate closed populations in contrast to the other studies which used either selected AI proven sires or random chosen groups of young unproven AI sires. Primary selection was for yield, but some studies included secondary selection for type.

These selection experiments were certainly not unique in that milk yield was the primary selection trait. However, they provided evidence for important scientific questions which were never explicitly asked; 1) Is the amount or rate of direct response consistent with theoretical expectation? 2) Did the selection reveal any serious negative correlated responses? 3) Are there benefits from selection on traits other than yield or will selection for yield be nearly as effective as selection on an index of yield and non-yield traits? 4) Can sufficiently divergent genetic groups be created which might show detectable differences in physiological, blood groups, biochemical, or immunological traits which may have some association with yield?

SELECTION RESPONSE - DIRECT AND CORRELATED

The researchers directing the studies in the NC-2 and S-49 projects recognized that the use of AI sires, either young or proven sires, is selection secondary to the selection practiced by AI organizations in choosing the parents of the young sires or the choice of proven sires from a candidate group of young sires obtaining progeny test information. However, the practical implication of the selection practiced was to give dairy producers an indication of results which might be obtained from various AI sire selection strategies for yield alone or yield jointly with a non-yield trait(s). Comparisons of the primary selected group with a control or alternative selection group generally showed differences (responses) which exceeded differences in the estimated genetic merit of sires of the respective groups (Pearson et al.; 1981; Meland et al., 1982; Croak-Brossman et al., 1982; Wilk and McDaniel, 1979). At an annual rate of 1.6% of the mean yield (108 kg), the selection line exceeded the random mating control over the 16 years of this closed population experiment (Legates and Myers, 1988). Selection for first lactation protein yield in a Holstein population generated a 4.9 kg increase in sire merit for protein yield in one generation of sire selection, corresponding to a

13.5% increase in protein yield of daughters (McAllister et al., 1990). Increases in sire genetic merit for milk yield and milk yield of daughters were 136 and 600 kg (9.6% of mean yields), respectively.

Several studies have reported correlated responses to selection in these experiments. Selection in Holsteins for yield alone versus yield and udder conformation resulted in a significant advantage for yield selection in milk yield, SNF yield, gross feed efficiency and net income per day and was accompanied by a decrease in milk component percentages and acceptable udder conformation (Pearson et al., 1981). No important differences in reproduction were found.

Two selection studies in Jerseys both showed significant increases in milk yield from selection of AI proven sires for yield compared to either random young sires in AI or random young bulls in the control line (Simerl et al., 1979; Wilk and McDaniel, 1979). A slight increase in size and weight of heifers was associated with the selection for yield (Simerl et al., 1979). In another selection study of Jerseys comparing AI proven sires with random young bulls, no differences were found in gross feed efficiency (Smother et al., 1986) or in mature size (Bonczek et al., 1992) but selection cows had significantly higher health care costs (Short et al., 1990). Days open were slightly greater for primiparous cows in the selected line (Bonczek et al., 1992a).

Increased feed efficiency (2.8%) was reported from selection of Holsteins for smaller body size and increased milk yield (Yerex et al., 1988). Greater health care costs for larger cows were associated with selection for larger size and increased milk yield (Mahoney et al., 1986). The Iowa study of Holstein sires chosen for high versus breed average genetic merit for milk yield showed 18% more lifetime profit for the high yield line (Bertrand et al., 1985). Minnesota investigators reported increased milk yield of daughters of bulls selected for high estimated genetic merit for milk yield compared to daughters of sires from the control line sires of average genetic merit for milk yield in 1964. However, this yield increase was accompanied by larger udders and related teat placement measurements (Petersen et al., 1985) and an increased health care cost which was more than offset by the increased income over feed cost (Hansen et al., 1979). Similar results regarding health care costs were found in the Iowa study where net return per lactation was 8 times the increased health care costs in the selection line (Shanks et al., 1978).

An economic measure was the defining comparison in the selection and crossbreeding study (McAllister et al., 1994). An annualized discounted net return (ADNR) was calculated for all pureline and crossline females born alive. These results showed almost a \$200.00 difference of the Holstein (H) line over the Ayrshire-based (A) pureline. The $H \times A F_1$ and an $(A \times H) \times [(A \times H) \times (H \times A)]$ second generation crossbred group had ADNR that exceeded the H line but were not significantly different. Joint estimation of additive and non-additive genetic effects on ADNR revealed significant heterosis (20.6%) and a cytoplasmic maternal effect favoring the A line (\$82) in addition to a direct additive effect which favored the H line (\$365).

IMPLICATIONS

Significant non-additive and cytoplasmic maternal effects for an overall measure of economic merit suggests that similar effects may exist within breed. If true, both selection and crossing between families, lines or breeds would need to be considered in breeding plans. Examining the full scope of available genetic avenues for dairy cattle improvement in light of

both new reproductive technology and the results of selection and crossbreeding experiments may prove very worthwhile.

Maximizing profit while controlling risk over a mix of planning horizons is the objective of each enterprise in the dairy industry. The ADNR per cow measure of profit in an enterprise considers both revenue and expenses as well as when they occur. ADNR can also combine capital and operating aspects. The ADNR of a herd can be subdivided into three components: 1) Overhead which does not vary between individual cattle, 2) germplasm trade in embryos, semen or live cattle, and 3) lifetime operating ADNR of individual cattle. Prices in germplasm trade depend heavily on expected lifetime operating ADNR of future female descendants. Reproductive rate, sex ratios and number of generations to realize the benefit will play an important role also.

Both additive and non-additive genetic effects contribute to the wide variation between cows in ADNR (McAllister et al., 1994). The economic value of milk yield is preeminent among dairy performance traits. Selection response whether estimated from selection studies reviewed earlier or estimated from studies of breeding populations (Van Vleck, 1988), clearly confirms the additive genetic variation available for exploitation. Heterosis, the primary source of non-additive genetic variation for milk yield, is only modest for individual lactation milk yield (McAllister, 1986). In contrast, the degree of heterosis for lifetime yields and lifetime profitability is quite high (McAllister et al., 1994; Touchberry, 1970). Non-additive genetic variation for reproductive and survival traits, which are major components of lifetime yield, are likely responsible.

Recent work has established the economic importance of herd life as being about one-third that of milk yield (Allaire and Gibson, 1992). Index selection using milk yield and key conformation traits associated with survival (Rogers, 1993) indicates a relative selection emphasis of yield to conformation traits of about 3:1 based on standardized selection index weights. Results of estimated ADNR of different purebred and crossbred groups based on results of the Canadian study (McAllister et al., 1994) are given in Table 1. The combination of complementary direct additive and cytoplasmic maternal additive effects and heterosis predicts a two breed rotational cross will be superior to the best pureline. Hence, knowledge of the genetics of ADNR and component traits is a critical element in designing breeding plans to maximize the profitability of the dairy herd and related industry enterprises. Current industry breeding practices appear to be largely insensitive to the recommended selection emphasis or the potential for combining selection and crossbreeding.

Breeding plans are affected profoundly by the mix of planning horizons and their relative emphasis. Risk increases dramatically as planning horizons move from short term through long term to planning for future centuries. Predicting consumer demand, relative prices and production systems in the distant future becomes very risky. Realizing the ADNR from breedings during one generation requires 7 to 10 years. Emphasis then is on maximizing total genetic merit for ADNR from existing germplasm resources. Realizing the ADNR from 10 to 15 generations of breeding requires 50 to 75 years. Accumulating additive genetic merit for future ADNR through selection will be an important component. Further study could examine the relative emphasis to place on using existing non-additive genetic variation and conserving germplasm with low current ADNR but with high ADNR of descendants several generations in the future.

Breeding strategies and plans of enterprises may differ widely based on their planning horizons. Knowledge gained from recent dairy cattle breeding and genetics research will be most useful in breeding plans for 1 to 15 generations or 10 to 75 years. Individual genes identified through molecular genetics studies may contribute to genetic improvement in ADNR (Schutz et al., 1993, Cowan et al., 1990). Breeding strategies should be flexible to take advantage of new knowledge in molecular genetic architecture.

Table 1. Estimated¹ ADNR² for pureline H³, F₁'s, RHMC⁴ and best TBRC⁵ relative to pureline A⁶.

| Genetic Group | ADNR(\$) |
|-------------------------------------|----------|
| H x H | 234.8 |
| H x A | 292.5 |
| A x H | 210.8 |
| RHMC (based on H x A) | 225.4 |
| Two Breed Rotational Cross (TBRC) | |
| Cycle 1 - H • H x A | 304.5 |
| Cycle 2 - A • H • H x A | 219.4 |
| Cycle 3 - H • A • H • H x A | 301.5 |
| Cycle 4 - A • H • A • H • H x A | 201.3 |
| Cycle 5 - H • A • H • A • H • H x A | 300.8 |

¹ Based on significant additive (H-A), heterosis, and cytoplasmic (H-A) genetic effects

² Annualized discounted net return

³ Holstein line

⁴ Repeated hybrid male cross

⁵ Two breed rotational cross

⁶ Ayrshire based line

Risk is inherent in all breeding plans. Knowing the sources of variation and the magnitude of their effects is the basis of designing breeding plans that control risk while maximizing genetic merit for ADNR. Risk is the variation in realized profit or ADNR around the expected or predicted value and can be positive or negative. Use of incorrect variables in defining ADNR along with incorrect relative prices or economic weights are elements of risk in the planning and prediction of response. The variation of true genetic merit for ADNR around the genetic index or the standard error of prediction (SEP) are the better known forms of risk. Random loss of desired genes and increased inbreeding are important sources of risk. Long term breeding programs in populations with small effective size are particularly vulnerable, even if they are global populations such as Holsteins. Random variation in genetic processes is an uncontrollable source of variation and risk.

Observations on biological and economic variables can provide a sound basis for predicting the ADNR of arbitrary relatives at some time in the future. So long as the economic or price aspects are uncorrelated with or not caused directly by biological variables, analyses can be separated. The framework for estimating phenotypic, genotypic or additive genetic merit for arbitrary relatives is well established (Henderson, 1984). Additive, non-additive, maternal, permanent environmental and residual (co)variance matrices among variables are critical input parameters.

Analyses of field collected data have provided sound estimates of such parameters for routinely recorded variables, such as yield of milk, fat and protein per lactation. Genetics and breeding research with experimental herds of dairy cattle has provided: 1) Verification that breeding plans using estimates of such parameters generate predicted direct and correlated responses, 2) Critical evidence on the likely importance of non-additive genetic covariation for economically important traits often indirectly through crossbreeding experiments, 3) Clear indications of which traits or variables might justify extensive field data study and, possibly more important, which can be ignored without serious impact, 4) Evidence on the economic importance of traits which are difficult to record in breeding herds (e.g. calf survival, health, longevity, growth), 5) Good first approximations of genetic parameters for economically or biologically important traits (feed intake, weight change, udder height).

The primary role of research herds is to study questions which can be examined only with great difficulty and expense in producer herds. The emphasis of producers on maximizing enterprise ADNR and controlling risk, precludes interference with breeding and management decisions that would have adverse economic impact on their herd. Experimental research has contributed significantly to breeding plans to maximize lifetime ADNR of dairy herds.

FUTURE RESEARCH

To be most beneficial, breeding research should anticipate the future and strive to provide knowledge not yet required. Current knowledge and expected results from current research must be integrated with rational predictions of future economic scenarios and production circumstances. Pressure will likely continue to improve economic efficiency. The lack of evidence for selection limits suggests selection for yield can and should continue. How much longer can the economic importance of survival and reproduction and the large non-additive genetic influence on them be largely ignored? Future research including field studies, experimental research and computer simulation should address questions of improving biological performance in an economic framework. Research from quantitative as well as molecular genetics must be allied to provide the new knowledge required.

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