

CONSEQUENCES OF SELECTION FOR WEANING WEIGHT ON THE
BIOECONOMIC EFFICIENCY OF BEEF CALF PRODUCTION

A thesis

Presented to

The Faculty of Graduate Studies

The University of Manitoba

by

Shah Amal

In partial fulfilment

of the requirements for the degree

DOCTOR OF PHILOSOPHY

1993



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Votre référence*

Our file *Notre référence*

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-85995-4

Canada

CONSEQUENCES OF SELECTION FOR WEANING WEIGHT ON THE
BIOECONOMIC EFFICIENCY OF BEEF CALF PRODUCTION

BY

SHAH AMAL

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

© 1993

Permission has been granted to the LIBRARY OF THE UNIVERSITY OF MANITOBA to lend or sell copies of this thesis, to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film, and UNIVERSITY MICROFILMS to publish an abstract of this thesis.

The author reserves other publications rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's permission.

ABSTRACT

Amal, Shah. Ph.D. The University of Manitoba, October 1993. **Consequences of selection for weaning weight on the bioeconomic efficiency of beef calf production.**

Major Professor; Gary H. Crow.

Consequences of selection for weaning weight, which is composed of direct and maternal components, on the efficiency of beef calf production were examined using a deterministic simulation model. Methods were developed to estimate relative genetic gain in the direct and maternal components of weaning weight after a single cycle of selection on weaning weight. Response for a Base Model was predicted using the classical theory of uniform rate of response to selection in discrete generations. A negative genetic correlation was assumed between the direct and maternal components of weaning weight based on the findings of a recent Canadian study. Sensitivity of response to a range of heritabilities, and correlation estimates that corresponded to the range reported in the literature, was simulated. This sensitivity analysis provided valuable information on the consequences of selection for weaning weight on direct, maternal and phenotypic response. Positive genetic correlation between the direct and maternal components resulted in maximum phenotypic response while negative genetic correlation resulted in minimum response. Correlated changes in the biological characteristics and economic output were computed to evaluate the bioeconomic efficiency of response to selection for weaning weight. Sensitivity of the bioeconomic input-output system to variation in the direct maternal correlation was also examined.

Positive genetic correlation between direct and maternal components of weaning weight was most advantageous in terms of improvement of bioeconomic efficiency. However, correlated changes in milk yield were dramatic. An examination of the partial efficiencies of the direct and maternal components showed that the maternal component was marginally superior in terms of bioeconomic efficiency. Sensitivity of bioeconomic input-output system to the assumed correlation between cow and calf characteristics was examined and used to moderate the results. Information on the hierarchical structure of the Manitoba beef cattle population was obtained from a survey carried out by the Manitoba Department of Agriculture. A gene-flow matrix describing the age-sex structure of the Manitoba beef cattle population was constructed using this information. Using the genetic parameters and bioeconomic considerations used in the Base Model, a Gene-Flow Model was developed. Bioeconomic response after a single cycle of selection at the beginning of the programme, was simulated for a period of 20 years. The Gene-Flow Model demonstrated that genetic improvement through selection at the beginning of the programme is not immediately passed to subsequent generations due to age differences in the selected group. The response stabilized or reached an asymptote around year 15 after a single cycle of selection in year one. This asymptotic response was equivalent to the uniform rate of response predicted by the classical Base Model. Response to selection for weaning weight was positive, though there was a genetic loss (decrease) in the maternal component due to the negative genetic correlation between direct and maternal components of weaning weight. The accumulated net discounted returns indicate that in a cow-calf basis, selection for weaning weight would be more beneficial

than no selection, even under negative genetic correlation between direct and maternal components of weaning weight. Though phenotypic and bioeconomic response was positive there was a clear reduction in milk yield.

TABLE OF CONTENTS

| | v |
|---|------|
| | Page |
| LIST OF TABLES | ix |
| LIST OF FIGURES | x |
| INTRODUCTION | 1 |
| REVIEW OF LITERATURE | 3 |
| Systems Approach to Animal Breeding Research | 3 |
| Maternal Effects | 4 |
| Genetic Control of Maternal and Direct Components of Weaning Weight | 7 |
| Antagonism Between Good Preweaning Environment and Subsequent Maternal Productivity | 8 |
| Milk Yield in Beef Cattle | 9 |
| Selection for Milk Yield | 11 |
| Prediction of Response | 12 |
| Gene-Flow Theory in Structured Populations | 13 |
| The Concept of Discounting | 15 |
| Economic Aspects of Selection | 18 |
| DEVELOPMENT OF METHODS | 19 |
| Estimation of Relative Genetic Gain for Embedded Traits | 19 |
| Sensitivity of Response to Selection | 21 |
| DESCRIPTION OF MODEL COMPONENTS | 22 |
| Genetic Considerations | 22 |
| Parameters used in the prediction of response to selection | 22 |
| Biological Considerations | 22 |
| Cow characteristics | 22 |
| Calf characteristics | 25 |
| Feed requirements of the cow-calf pair | 26 |

| | |
|---|----|
| Cow feed requirements | 26 |
| Calf feed requirements | 29 |
| Chronology of Events Through the 365 Day Cow-calf Cycle | 30 |
| Period 1 | 31 |
| Period 2 | 31 |
| Period 3 | 31 |
| Period 4 | 32 |
| Economic Considerations | 32 |
| Partial Efficiency | 33 |
| Describing Gene-Flow in a Population | 34 |
| Gene-Flow in hierarchial populations | 44 |
| Describing a Hypothetical Structured Population | 47 |
| Bulls in the nucleus sector | 47 |
| Nucleus bulls to mate commercial cows | 49 |
| Commercial bulls to mate commercial cows | 49 |
| Commercial cows | 50 |
| Parameters Used in the Prediction of Response to Selection | 50 |
| Simulation of Response to Selection | 50 |
| Biological and Economic Considerations | 52 |
| RESULTS AND DISCUSSION | 53 |
| Base Model | 53 |
| Phenotypic response to selection | 53 |
| Sensitivity of Response to Selection | 53 |
| Heritability of direct component equals heritability of maternal component | 55 |
| Heritability of direct component larger than heritability of maternal component | 58 |

| | |
|---|-----|
| | vii |
| Heritability of maternal component larger than heritability of direct component. | 58 |
| Correlated Changes in Biological Characteristics due to Selection on Weaning Weight | 61 |
| Changes in calf characteristics | 62 |
| Changes in cow characteristics | 62 |
| Biological and Economic Efficiency | 65 |
| Partial Efficiency | 65 |
| Partial efficiency of the direct component of weaning weight | 66 |
| Partial efficiency of the maternal component of weaning weight | 66 |
| Partial efficiency of the direct and maternal components of weaning weight | 68 |
| Sensitivity of Bioeconomic Considerations to $\Gamma_G: wwd, wwm$ | 71 |
| Sensitivity of calf characteristics | 72 |
| Sensitivity of cow characteristics | 72 |
| Sensitivity Analysis of Bioeconomic Considerations to the Relationship between Calf and Cow Characteristics | 75 |
| Sensitivity to a Unit Change in the Direct Component | 76 |
| Sensitivity to biological and economic characteristics | 76 |
| Sensitivity to a Unit Change in the Maternal Component | 77 |
| Sensitivity to biological and economic characteristics | 77 |
| Sensitivity to a Unit Change in Direct and Maternal Components | 79 |
| Sensitivity to biological and economic characteristics | 79 |

| | |
|--|------|
| | viii |
| Gene-Flow Model | 79 |
| Response to selection | 80 |
| Changes in Biological and Economic Characteristics | 83 |
| Changes in calf characteristics | 83 |
| Changes in cow characteristics | 85 |
| SUMMARY AND CONCLUSIONS | 88 |
| LITERATURE CITED | 93 |

LIST OF TABLES

ix

| Table | Page |
|---|------|
| 1. Proportion of genes derived from yearling males selected at time 0, over 20 years. | 38 |
| 2. Total (ΔG_{WW}), direct (ΔG_{WWD}) and maternal (ΔG_{WWM}) responses in weaning weight. | 44 |
| 3. Responses to selection with base set of assumed genetic parameters ($h^2_D=0.4$, $h^2_M=0.2$, $r_{G:WWD,WWM}=-0.4$). | 54 |
| 4. Sensitivity of response to selection. | 56 |
| 5. Changes in cow and calf characteristics due to selection for weaning weight. | 63 |
| 6. Partial efficiency of the direct component of weaning weight. | 67 |
| 7. Partial efficiency of the maternal component of weaning weight. | 69 |
| 8. Partial efficiency of the direct and maternal component of weaning weight. | 70 |
| 9. Changes in cow and calf characteristics | 73 |
| 10. Percent change in cow and calf characteristics | 74 |
| 11. Sensitivity of cow and calf characteristics to a unit change in the direct component of weaning weight. | 77 |
| 12. Sensitivity of cow and calf characteristics to a unit change in the maternal component of weaning weight. | 78 |
| 13. Sensitivity of cow and calf characteristics to a unit change in the direct and maternal component of weaning weight. | 80 |
| 14. Changes in cow and calf characteristics for the last year (Year 20) of the evaluation period. | 84 |
| 15. Discounted returns per calf from a single cycle of selection. | 86 |

LIST OF FIGURES

x

| Figure | Page |
|---|------|
| 1. Path diagram of direct and maternal components of weaning weight. | 6 |
| 2. Plot of simulated milk yield. | 27 |
| 3. Proportion of genes from males selected in time zero over over 20 years. | 39 |
| 4. Response from a single cycle of selection in the nucleus sector. | 41 |
| 5. Flow diagram of direct (ΔG_{WWD}), maternal (ΔG_{WMM}) and total (ΔG_{WW}) responses. | 43 |
| 6. Total (ΔG_{WW}), direct (ΔG_{WWD}) and maternal (ΔG_{WMM}) responses in weaning weight after a single cycle of selection in the nucleus sector | 45 |
| 7. Gene-flow in a two tier population structure. | 48 |
| 8. Schematic of matrix (P) describing gene-flow in the Manitoba beef cattle population. | 51 |
| 9. Sensitivity of response to selection: Heritability of direct component ($h^2_D=0.2$) equals heritability of maternal component ($h^2_M=0.2$). | 57 |
| 10. Sensitivity of response to selection: Heritability of direct component ($h^2_D=0.4$) larger than heritability of maternal component ($h^2_M=0.2$). | 59 |
| 11. Sensitivity of response to selection: Heritability of maternal component ($h^2_M=0.4$) larger than heritability of direct component ($h^2_D=0.2$). | 60 |
| 12. Plots of calf forage dry matter consumption (ClfFI) and calf milk dry matter consumption (ClfMI). | 64 |
| 13. Response in weaning weight (WW) from a single cycle of selection. | 82 |
| 14. Discounted returns from a single cycle of selection. | 87 |

INTRODUCTION

Selection based on measurements of growth has been, and continues to be, the focus of beef cattle improvement programmes in many parts of the world. In some countries, selection on preweaning growth, especially weaning weight, has received more attention due to its close association with cow-calf efficiency. It is well established that growth during the preweaning period is affected both by the calf's own growth potential (direct) effects and the maternal environment (maternal) effects provided by its dam. The direct and maternal components of weaning weight are known to be genetically correlated (Meyer 1992).

There are few reports in the literature on the bioeconomic effects of selection for preweaning growth on cow-calf efficiency. This is due to the lack of knowledge on genetic and biological parameters of the calf's preweaning growth, and its genetic and biological association with traits expressed by the dam. There is a clear need, therefore, for simulation studies on beef calf production efficiency (input-output) systems, especially in the context of selection for weaning weight (Barlow 1978; Harris 1970; Harris et al. 1984).

Sensitivity analysis of the various genetic and biological parameters of the calf and the relationship with traits expressed by its dam should provide valuable information on sensitivity of the model to poorly defined parameters and moderate the results of the simulation study. Beef cattle populations have overlapping generations, therefore response predicted as a result of a single cycle of selection for weaning weight at the

beginning of a selection programme takes many generations to equal the rate of response predicted by the classical theory of uniform rate of response. Prediction of response for a trait like weaning weight of beef cattle is therefore not straightforward. This research therefore focuses on the consequences of selection for weaning weight on the bioeconomic efficiency of beef cattle production.

The objectives are:

- 1) To develop a model representing a cow-calf production system with special attention to cow forage intake and calf forage intake and calf milk yield intake.
- 2) To determine correlated responses in cow and calf traits due to selection on weaning weight and to evaluate economic returns.
- 3) To determine sensitivity of results to assumed parameters - heritability of direct and maternal components of weaning weight, the genetic correlation and biological association between calf and cow traits.
- 4) To determine economic value of response over time with discounted returns in a Gene-Flow model.

REVIEW OF LITERATURE

Systems Approach To Animal Breeding Research

Integration of ideas and techniques from different scientific disciplines is important for human progress. This integration of ideas and conceptualization of production systems in systematic mathematical terms has been variously called systems analysis, simulation and computer modeling (Smith and Harrison 1978; Cartwright 1978; Wilton 1979; Csaki 1985; Harris et al. 1984, 1986; Bourdon 1988). Genetic experimentation with livestock species is very complex, expensive and time consuming. Computer modeling lends itself to mathematical description of these complexities. Systematic mathematical description allows the development of a complete systems objective for more accurate and comprehensive decision-making.

Animal breeding, being a highly quantitative science, facilitates computer modeling (Csaki 1985). Simulation is a practical approach in designing proper animal breeding programmes which involve the integration of several subsystems. It therefore complements and enhances the knowledge of animal genetics obtained from animal breeding experiments. Animal geneticists used simulation studies as early as 1956 (Harris and Stewart 1986). The capacity to simulate 'real world conditions' of livestock production has increased tremendously with modern computers of today and has provided better understanding of the sciences of animal genetics, statistics and management (Cartwright 1970; Cartwright 1978; Harris and Stewart 1986; Bourdon 1988; Lamb et al. 1992).

Maternal Effects

In mammals, where there is a close association among family groups, a trait like weaning weight (WW) is composed of several conceptual components. In beef cattle such a relationship exists between an offspring and its dam. Growth during this preweaning period is affected both by the offspring's own growth potential and the maternal environment provided by its dam. The maternal influence provided by the dam is strictly environmental relative to the offspring. The difference among the dams in their expression of the maternal influence is partly genetic and partly environmental. The existence of maternal effects has been known as far back as 66 B.C. (Robison 1981) and its importance in selection decisions has been recognized by the earliest animal breeders.

The first theoretical model for traits with maternal and growth components was described by Dickerson (1947). Koch and Clark (1955) used path coefficients to describe the association amongst beef cattle groups in terms of maternal and growth components. The model proposed by Willham (1963) is an extension of the earlier model of Dickerson (1947) and is widely accepted today. The model is best described in terms of an individual (i) and its association with its dam (j). This relationship may be described with linear models as follows:

$$P_{wwi} = \mu + G_{wwi} + E_{wwi} \quad (1)$$

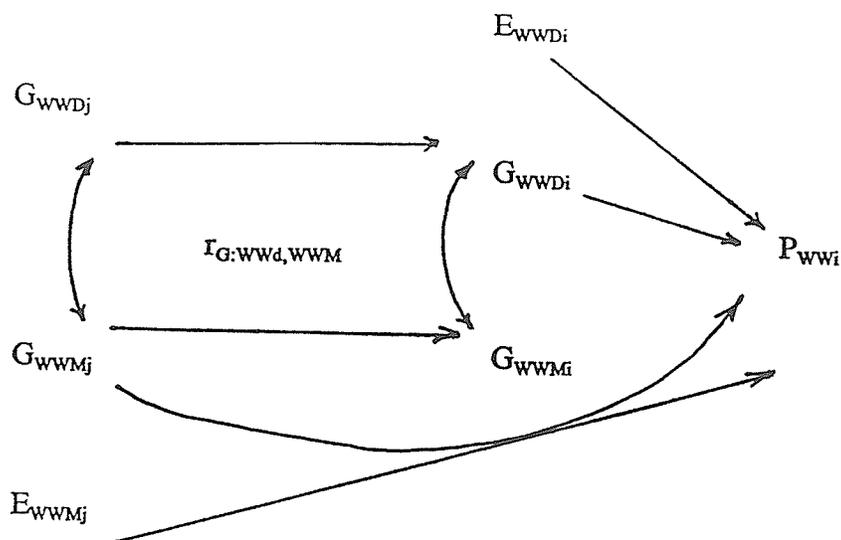
where, μ is the mean value for weaning weight, P_{wwi} is the phenotype for weaning weight, G_{wwi} is the additive genetic value of an individual for preweaning growth often

referred to as the direct genetic effect, and E_{WWDi} is the environmental effect on this trait (this also includes non-additive genetic variation). Equation 1 can be rewritten as:

$$P_{\text{WWDi}} = \mu + G_{\text{WWDi}} + G_{\text{WWMj}} + E_{\text{WWDi}} + E_{\text{WWMj}} \quad (2)$$

In this expression P_{WWDi} of an individual (eg. a calf) is influenced by four major components, G_{WWDi} often referred to as the direct genetic effect, G_{WWMj} is the maternal effect of the genotype of the individual's dam, E_{WWDi} is the effect of the calf's non maternal environment and E_{WWMj} is the effect of the environment on the maternal value of the dam. The effect of direct and maternal components on weaning weight phenotype are illustrated in the path diagram shown in Figure 1. The four paths directed at P_{WWDi} represent the four factors in equation 2 above. The path diagram also allows for the possibility of a genetic correlation ($r_{G:\text{WWD},\text{WWM}}$) between the direct and maternal effects. As with most biological phenomena, the true underlying model is seldom known and various extensions to that shown in Figure 1 have been proposed, including models with grand maternal effects (Hohenboken 1985). Most recent research in this area has used a model very similar to that in Figure 1.

The maternal environment affecting a trait like weaning weight is itself composed of several factors. These include cytoplasmic effects from maternal mitochondria in the egg, the prenatal maternal influence (intrauterine environment) and the postnatal maternal environment (milk yield/mothering ability). The importance of these maternal factors have been highlighted by many researchers (Koch 1972; Legates 1972; Bradford



P_{wWi} = Phenotype of animal (i) of dam (j)

G_{wWd_i} = Direct genetic effect

G_{wWm_j} = Maternal genetic effect

E_{wWd_i} = Direct environmental effect

E_{wWm_j} = Maternal environmental effect

$r_{G:wWd,wWm}$ = Genetic correlation between direct and maternal components

Figure 1. Path diagram of direct and maternal components of weaning weight.

1972; Robison 1972; Hohenboken and Brinks 1981; Hohenboken 1985; Meyer 1992). Milk production appears to be the most important maternal factor (Hohenboken 1985; Freking and Marshall 1992; Jenkins and Ferrel 1992) and will form the basis of most of the discussion in this review.

Accurate prediction of response to traits composed of maternal and direct components is not straightforward (Willham 1980). Only females express the maternal trait (sex limited), thus genetic changes in maternal effects are expressed one generation later than genetic changes in direct effects. Maternal effects may also be genetically and environmentally correlated with direct effects. This association between maternal and direct components of weaning weight has important implications to selection programmes.

Genetic Control of Maternal and Direct Components of Weaning Weight

In general the literature indicates that direct and maternal components of weaning weight are moderately heritable. Up until 1975, estimates were obtained entirely from designed experiments under research station environments. From these studies, the maternal genetic variation appeared to be slightly larger (0.46) than the genetic variation in the direct component of weaning weight. The maternal genetic values ranged from 0.51 to 0.34, while the direct genetic value ranged from 0.32 to 0.23 (Hill 1965; Desse and Koger 1967; Hohenboken and Brinks 1981; Koch 1972). All these experiments reported a larger negative correlation between the direct and maternal components with the exception of the work of Hill (1965) which showed a positive correlation during the early

part of the preweaning period (between 90 and 120 days of age).

With the advent of modern computers and new evaluation techniques, researchers estimated genetic parameters of weaning weight and preweaning gain from field data. Wright et al. (1987) estimated genetic parameters for weaning weight and its two components for the Simmental cattle population in the United States from a large field data source (114,899 records). Low heritability values were reported for both the components with the direct component having a slightly larger (0.12) value than the maternal (0.09) component. The genetic correlation between the direct and maternal components of weaning weight ($r_{G:WWD,WWM}$) was slightly positive (0.16) which is contrary to many earlier reports in the literature. More recently Trus and Wilton (1988) reported estimates of genetic parameters for maternal traits for 5 breeds (Angus, Hereford, Shorthorn, Charolais, and Simmental) cattle in Canada. Eleven years of data comprising 409,053 records were used in this study. For preweaning gain, both the components were moderately heritable with the direct component larger (.36) than the maternal component (.22). In agreement with many of the earlier reports $r_{G:WWD,WWM}$ was found to be strongly negative (averaging -0.36) for most of the breeds.

Antagonism Between Good Preweaning Environment and Subsequent Maternal Productivity

From a series of designed experiments conducted to study maternal effects in beef cattle Mangus and Brinks (1971) reported that good preweaning environment for the beef heifer (a good supply of milk from its dam) resulted in its subsequent poor maternal

performance by the heifer when she became a mother. Robison (1971), Baker 1980 and Robison 1981 also made similar conclusions. Willham (1972) suggested that heifers suckled by dams with higher milk yield are very likely to deposit excess fat in their mammary gland. This would consequently result in reduced milk production of heifers, particularly in their first lactation, and lower calf weaning gains.

In contrast Irgang et al. (1985) have reported favourable correlated responses to selection for milk yield, preweaning and postweaning traits. In this long term experiment Hereford bulls from a common base population were selected to form three distinct lines (i.e. control line selected at random, weaning gain line selected for increased weaning weight and postweaning gain line selected for increased postweaning gain. Their results do not suggest the existence of a negative environmental correlation between any of these traits. On the contrary, milk yield in cows was genetically positively correlated with weaning weight and postweaning gain. In support of their finding they refer to the suggestion made by Sejrsen (1978) that animals with high growth potential also have a high growth hormone concentration. The presence of high growth hormone concentrations in the blood stimulates better mammary tissue growth which can accommodate the milking potential of the cow. Heifers with high growth potential when suckled by dams with good maternal ability would themselves be excellent mothers.

Milk Yield in Beef Cattle

Maternal performance of beef cows interacts both biologically and economically with other beef production traits like growth rate. It is directly related to preweaning growth

rate and weaning weight of the calf. Milk yield forms the primary component of the maternal environment provided by the beef cow. The milk production of the dam is partly genetically determined. There are few reports in the literature on the milk production of different beef breeds. Daily milk production for beef breeds range from 1.00-8.73 kg per day (Gifford 1949; Melton et al. 1967; Bond and Wiltbank 1970; Notter et al. 1978; Reynolds et al. 1978; Rutledge et al. 1981; Wilton and Mondragon 1981; Beal et al. 1990). The phenotypic correlation between total milk production and calf weaning weight has been reported to be high and in the range of 0.5 to 0.8 (Gleddie and Berg 1968; Jeffery and Berg 1971; Marshall et al. 1976; Reynolds et al. 1978; Mondragon et al. 1983).

All these reports clearly indicate that milk yield alone is an adequate measurement of the dam's lactation influence on calf gain. Thus the dam's milk yield could be used as a good predictor of the calf's weaning gain. The regression of calf weaning weight on average milk yield has been computed by a number of workers (Jeffery and Berg 1971; Marshall et al. 1976; Spelbring et al. 1977; Butson et al. 1980; Wilton 1979; Mondragon et al. 1983). Measurements of lactation from the University of Alberta beef herd were used by Butson et al. (1980) to study factors influencing weaning weight. Their regression equations showed that an increase of 1 kg in average daily milk yield increased weaning weight by 7.7 kg. Bogg et al. (1980) also reported a similar value (7.20 kg). Wilton (1979) reported a higher value (9.7 kg) while Mondragon et al. (1983) reported a lower value (4.6 kg).

Selection for Milk Yield

From these studies it seems that there is potential to increase average milk production of beef cows, especially that of British beef breeds. Wilton and Mondragon (1981) have suggested that selection for maternal ability through the Record of Performance programmes would increase weaning weights of beef calves since weaning weight is significantly associated with milk yield. Many researchers have examined reasonable goals for milk yield in the commercial beef cattle production system. As milk production interacts biologically with other traits, selection for increased milk production must be viewed in an economic context. Notter et al. (1979) used a computer simulation model to investigate the effects of the level of milk production on bioeconomic efficiency in a cow-calf-feedlot management system. Their study indicated that increased milk production improved bioeconomic efficiency with the optimum level of milk production influenced by the differences in feed prices at the feedlot and commercial cow-calf operation. Diverse breed types were used by McMorris and Wilton (1986) to study the bioeconomic efficiency of milk production and cow weight at the farm level. In contrast to the study of Notter et al. (1979) increased milk yield had no obvious effect on gross margin. The cows used in this experiment, however, were fed purchased corn silage. This may not truly reflect the feeding practices of a typical beef cow-calf operation in Canada where cows are pastured for a greater part of the lactation period and generally fed silage hay in the barn. The bioeconomic effects of milk yield was much more positive when the feed price was decreased. When overhead expenses, carcass discounts and retail yield premiums were considered cows with higher milk yield were clearly

advantages to the beef cattle farm. Clutter and Nielsen (1987) recently concluded a long term study on beef cows with different genetic potentials for milk production. The cows used in this experiment were similar in growth rate and mature size in an attempt to compare efficiency of beef production at different milk production levels. Though no economic evaluation was conducted the results conclusively showed that higher level of milk intake by the calves resulted in a significant increase in weaning weight. This increase in weaning weight was maintained throughout the postweaning period in the feedlot. Final weight and carcass weight of the calves also reflected this advantage.

Prediction of Response

Van Vleck et al. (1977) were the first to describe and evaluate prediction of response to selection for maternal and direct components of weaning weight in beef cattle. In their simulation study they used various combinations of records for male and female selection schemes in their population. While selection of males was only for the growth component, females were selected for either one of the components or both. The selection intensity in the male population was higher ($i=1.25$) than in the female population ($i=0.60$). Response was simulated for a highly negative genetic correlation ($r_{G:WWD,WWM}=-0.87$) and for a genetic correlation close to zero ($r_{G:WWD,WWM}=-0.06$). One major assumption made in their study was that generations were discrete and not overlapping. There was no change in the predicted phenotypic mean of weaning weight after 5 generations of selection where a highly negative genetic correlation was assumed. However, when the genetic correlation was close to zero there was an increase in

predicted phenotypic response. This clearly indicates the dependence of selection response in weaning weight on the magnitude of $r_{G:WWD,WWM}$.

Gene-Flow Theory for Structured Populations

Prediction of response to selection for traits composed of direct and maternal components when generations overlap is not straightforward. One of the conditions generally assumed in prediction of response to selection is that individuals of a population group belong to a distinct generation. Such generations are said to be discrete as individuals of different generations do not interbreed. This is only true for annual plants and with many insect species which interbreed only in the same generation. In farm animal populations however generations are usually not discrete. There is commonly a continuous range of animal ages in the production system and individuals of different age groups interbreed.

The theory for predicting rate of response to artificial selection in livestock population was first developed by Dickerson and Hazel (1944) and later generalized by Rendel and Robertson (1950). This theory came to be known as the 'classical' or 'asymptotic' theory. The formulae used in predicting rate of response to selection assumes the same selection scheme is practised each generation. With the overlapping generations in animal populations, the rate of response predicted by the classical theory is only reached asymptotically. Hill (1974) presented a matrix version of the gene flow theory. This theory further generalizes the ideas of Dickerson and Hazel (1944) and allows exact prediction of response to selection. The matrix methodology also enables

a more complete description of the population structure. It specifies the passage of genes through the various sex and age subclasses and population strata. Most importantly it permits prediction of response to selection before the asymptotic response is reached.

Within a species animals of different age groups breed together and contribute toward the genetic change of the population. With domestication of farm animals man not only determines which individuals are allowed to produce the next generation but also decides the genetic demography (structure) of the population. The degree of control over this structure varies among species. In poultry, for example, the corporate breeding companies arrange the structure of nucleus and multiplier breeders for their own purposes. Beef cattle lie at the other end of the scale in terms of organization of the breeding population, since many normally independent breeders contribute breeding stocks to the commercial industry. Yet even here, the market economy in breeding stock among breeders has produced a hierarchial type of structure. Livestock populations are known to be structured and show hierarchial organization. Such a structure in domestic animals was first described by Robertson (1953) for cattle. Many others have discussed this issue since, Barker and Davey (1960); Davey and Barker (1963); Ozkutuk and Bichard (1977); Toll and Barker (1979); Koots and Crow (1990) and Gearheart et al. (1990).

All these studies reveal a hierarchial breed structure with two or more distinguishable strata. The hierarchic breed structure may be visualized as a pyramid. In its simplest form the pyramid is made up of two strata. The upper stratum is made up of a small elite group of animals from the purebred herds commonly called the

nucleus group. This group is an elite group of herds and usually does not acquire breeding animals from the lower stratum of the population. Genetic improvement in the nucleus stratum is through selection of male breeding animals within the nucleus. Only about 5% of the beef cattle population in North America are considered to belong to this group (Koch et al. 1986; Willham et al. 1986). Genetic improvement in the population is through the dissemination of genes (genetic superiority) from the nucleus stratum to commercial stratum. In a closed breeding population, sires from the lower commercial stratum even when superior to the poorest sires in the upper stratum would not be used for breeding in the pure bred herds occupying the nucleus stratum. Researchers in Australia and New Zealand have proposed an open nucleus system that allows for the use of superior commercial sires in the upper nucleus stratum. Such a system is anticipated to bring about greater genetic progress and increased profit to the sheep industry (Rae 1982).

The Concept of Discounting

As discussed earlier, generations in beef cattle populations overlap, therefore genetic responses fluctuate in the early years of any selection program. These fluctuations in early genetic response can be very large. These differential expression of genetic improvement from selection can be expressed equitably with some common denominator. A standard technique in management accounting, commonly called the Net Present Value (Discounted Cash Flow) procedure allows for the conversion of monetary returns of future years into a single present value (Boehlje and Eidman 1983). A detail discussion

on the Discounted Cash Flow Method can be obtained from any major text on management accounting.

A brief account is given here as it relates to animal breeding. The idea of the discounted cash flow method is based on the concept that an economic benefit of some investment is more valuable at the present time compared with its value deferred to sometime in the future. So it is simply a time-related concept. This concept put in mathematical terms is:

$$NPV = [1/(1+R)]^k \quad (3)$$

where, NPV is net present value of one dollar obtained, k is years from the present, and r is the interest rate. The concept of net present value is actually the inverse of the compound interest concept. It found its first use in animal breeding selection programmes with the paper of Poutous and Vissac (1962) who did a theoretical study of economic gains in progeny testing of artificially inseminated bulls. Since then this concept has been well accepted by the animal breeding research community and is frequently used to predict financial gains of selection programmes (Soller et al. 1966; Hill 1971; Hinks 1971; James 1972; Petersen et al. 1974; Hill 1974; Brascamp 1975; Cunningham and Ryan 1975; Everett 1975; Mitchell et al. 1982; Simm et al. 1987). The interesting aspect of the technique is that it lends itself to monetary evaluation of trends of genetic response over time to selection when generations overlap. Benefits in early generations are least discounted and thus would make a larger contribution to the total

discounted monetary return. It also provides a simple solution for appropriate evaluation of current breeding programmes discounting all future returns to their present value.

There is, however, disagreement in the preference of the discount rate used in the calculation of monetary returns for appraising selection programmes. This disagreement is not entirely an issue of workers in animal breeding alone. There are two major schools of thought amongst economists on this important economic evaluation technique. One school of thought regards the discount rate in terms of social time preference, a rate that allows for comparison of alternative investment choices over time in the general interest of the people. Griliches (1955) wrote an exhaustive review on the application of the discounting technique to corn breeding. The other school of thought considers discount rate in terms of proper allocation of limited resources of a nation between the private and public sectors of its economy. This discount rate is commonly referred to as the social opportunity cost rate and is similar to the cost of borrowing money in the financial circles.

This difference of opinion on the choice of the discount rate remains largely unresolved. Among animal breeders, there seems to be, however, a recent consensus that future returns and costs of animal breeding projects be discounted at a social time preference rate of 4% (Bird and Mitchell 1980; Mitchell et al. 1982). Such a rate is considered to be inflation free and includes some allowance for risk and uncertainty. Smith (1978) showed that a practical and simpler way of evaluating selection programmes is to calculate the stream of discounted benefits over many years from a single cycle of selection in year one.

Economic Aspects of Selection

The ultimate aim of any production system is to make profit. Selection programmes may be viewed as long term means of increasing productivity of livestock production systems. Thus the goal of any breeding program in animal agriculture is to identify and select animals with specific trait or traits as parents of the next generation. These animals are expected to contribute towards an overall efficient, viable and profitable production system. Thus the most important and the most difficult task is defining and deciding the selection program for a production system that would bring about maximum profit. It is therefore very important to evaluate the economics of alternative selection goals before making recommendations to the industry that may bring about maximum returns (Long and Fitzhugh 1970; Cartwright 1978; Harris 1970; Foster et al. 1984; Harris et al. 1986; Lamb et al. 1992).

These alternative selection decisions may be translated to individual animal profit margins in terms of inputs and outputs. This bioeconomic approach would place selection programmes on a more practical perspective, especially for traits like weaning weight, which is composed of both direct and maternal components. The main objective of this study is to evaluate the consequences of selection for weaning weight on the bioeconomic efficiency of beef cattle production.

DEVELOPMENT OF METHODS

Estimation of Relative Genetic Gain for Embedded Traits

Prediction of phenotypic response for traits with direct and maternal components is not straightforward, as discussed in the review of literature. The rate of response to selection for such embedded traits is proportional to the regression of the genotype of both the direct and maternal components on the phenotype (Dickerson 1947). Genetic selection differentials for each of these components is then the phenotypic selection differential multiplied by the regression of the breeding value of the individual components on phenotype (Van Vleck 1973). To estimate the genetic response for the direct and maternal components of weaning weight, their respective genetic covariances with the phenotypic selection criterion have to be determined. For direct genetic effects (G_D), this covariance is:

$$\text{COV} (G_{D\alpha} \cdot P_{WWI}) = a_{\alpha i} \sigma_{G:WWD}^2 + a_{\alpha j} \sigma_{G:WWD, WWM} \quad (4)$$

and for maternal genetic effects (G_M), the covariance is:

$$\text{COV} (G_{M\alpha} \cdot P_{WWI}) = a_{\alpha i} \sigma_{G:WWD, WWM} + a_{\alpha j} \sigma_{G:WWM}^2 \quad (5)$$

where, $a_{\alpha i}$ and $a_{\alpha j}$ are coefficients of relationships between the animals used for evaluation. The subscript α in the above expressions refers to the individual being

selected; i refers to the individual expressing the phenotypic record used as the selection criterion; and j refers to the dam of individual i . The variances are additive genetic variances for direct ($\sigma^2_{G:WWD}$) and maternal ($\sigma^2_{G:WWM}$) effects on weaning weight and then genetic covariances ($\sigma_{G:WWD,WWM}$). Details of deriving these coefficients has been described by Willham (1963). To calculate the genetic gain for each component of weaning weight, it was assumed that selection was based on the record of the animal's own performance i.e. a_{ai} is the coefficient of relationship between the individual being selected and the individual expressing the phenotypic record (i.e. $a_{ai}=1$) and a_{aj} is the relationship of the dam of individual i to individual a . These coefficients were substituted into the respective covariances (Equations 4 and 5) to obtain the formulae to calculate genetic gain for each component of weaning weight. The formula to calculate direct genetic gain is:

$$\Delta G_{WWD} = [h^2_D + (r_{G:WWD,WWM} h_{WWD} h_{WWM})/2] I \sigma_{P:WW} \quad (6)$$

and the formula to calculate maternal genetic gain is:

$$\Delta G_{WWM} = [(r_{G:WWD,WWM} h_{WWD} h_{WWM}) + h^2_M/2] I \sigma_{P:WW} \quad (7)$$

where, h^2_D is heritability of the direct effect, h^2_M is heritability of maternal effect, $r_{G:WWD,WWM}$ is the genetic correlation between the direct and the maternal effect on weaning weight, I is the selection intensity, and $\sigma_{P:WW}$ is the phenotypic standard

deviation of weaning weight.

Sensitivity of Response to Selection

In general, the literature indicates that direct and maternal components of weaning weight are both moderately heritable. Estimates from the literature from designed experiments report a negative $r_{G:WWD,WWM}$ (Barlow 1978). A summary of reports of genetic parameters for weaning weight and its components from field data was reported by Meyer 1992. Trus and Wilton (1988) were the first researchers in Canada to report genetic parameters of maternal traits for beef cattle based on field data. Eleven years of data comprising 429,053 records were used in their analysis. In agreement with many of the earlier reports based on designed experiments, the $r_{G:WWD,WWM}$ relation was found to be highly negative. From a Canadian perspective, these estimates are the most recent and most reliable given the large number of records used in their analysis. There are many other reports in the literature with contrasting estimates of genetic parameters of weaning weight (Wright et al. 1987; Johnson et al. 1992; Cantet et al. 1992; Meyer 1992). There are suggestions of significant breed differences for genetic parameters of maternal traits in beef cattle (Johnson et al. 1992; Meyer 1992).

DESCRIPTION OF MODEL COMPONENTS

Genetic Considerations

Parameters used in the prediction of response to selection. The heritability assumed for weaning weight was 0.30, for the direct component, 0.40, and for the maternal component, 0.20. The genetic correlation between the growth and maternal components was assumed to be -0.40. All these assumed parameters were adapted from the work of Trus and Wilton (1988). In the Canadian context, these estimates are the most recent and most reliable. Eleven years of data comprising 429,053 records were used to compute these estimates. The phenotypic standard deviation for weaning weight was 29 kg. A selection intensity of 2.34 for males was assumed which represents the limit of what could be achieved in practice.

Biological Considerations

For each year cycle (365 days) daily feed requirements for the cow-calf pair was calculated. Certain initial parameters based on averages obtained from the literature were assumed. Bioeconomic comparisons were then computed as changes to these initial constants.

Cow characteristics. Beef cows were assumed to survive up to a maximum of 9 parities. A similar assumption on maximum survivability was made by Rogers (1972) in his simulation study. Death losses in the cow population were based on survival rate between parities of 90%. The following equation describes the proportion of cows in

each age group, these proportions sum to unity.

$$0.9x + 0.9^2x + 0.9^3x + 0.9^4x + 0.9^5x + 0.9^6x + 0.9^7x + 0.9^8x = 1 \quad (8)$$

where x is the proportion of the cow herd that is replaced by two year old females each year, for example:

$$0.9x + 0.81x + 0.729x + 0.656x + 0.590x + 0.0531x + 0.478x + 0.478x = 1$$

$$x = 0.195$$

Age distribution of each cow parity group is calculated as a percentage of the total reproducing cow population, so for $x = .195$, there is the following distribution of cows:

| Age group | % of total population |
|-----------|------------------------|
| 2 | $(0.900x) 100 = 17.56$ |
| 3 | $(0.810x) 100 = 15.80$ |
| 4 | $(0.729x) 100 = 14.22$ |
| 5 | $(0.656x) 100 = 12.80$ |
| 6 | $(0.590x) 100 = 11.52$ |
| 7 | $(0.531x) 100 = 10.37$ |
| 8 | $(0.478x) 100 = 9.33$ |
| 9 | $(0.430x) 100 = 8.40$ |

The age distribution of beef cows computed by this method corresponds closely to that reported in the literature by Wilton and Morris (1976) and Long et al. (1975). This age

distribution was used to calculate the weighted average mature cow body weight for the population (Weinbach 1941; Brody 1945). Growth curve parameters, B (0.930) and k (0.190) obtained from the work of Goonewardene et al. (1981) were used with Brody's growth equation $Y_t = A(1-Be^{-kt})$. A mean cow weight of 500 kg characterizing a medium frame beef cow was assumed for year zero. Long et al. (1975) and Wilton et al. (1974) used a similar approach to characterize the weights of cows in their simulation work.

| | | | | | | | | |
|-----------|-----|-----|-----|-----|-----|-----|-----|-----|
| Age group | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Weights | 401 | 454 | 479 | 490 | 495 | 498 | 499 | 500 |

(9)

Using these predicted weights and equilibrium percentage of cows in each age group, a weighted average cow weight was calculated.

$$\{17.6(401) + 15.8(454) + 14.2(479) + 12.8(490) + 11.5(495) + 10.4(497) + 9.3(497) + 8.4(500)\}/100 \quad (10)$$

This weighted average was 470 kg. Average gain of cows was also calculated as a weighted average of individual gains of each age group. Average daily cow milk production was assumed as 6.4 kg from the work of Gleddie and Berg (1968). This value closely resembled "medium milkers" reported by McMorris and Wilton (1986), and Clutter and Nielsen (1987).

Change in the direct component of weaning weight reflects the response to selection for preweaning growth. An increase in this component of weaning weight is expected to increase cow mature weight. Mrode (1988) suggested that evidence from the literature on correlated response in cow weight is sketchy. Olthoff et al. (1990) have reported an average increase in cow weight of 1.6 kg per year to selection for yearling weight. Scaling weaning weight to cow mature weight would result in a 1-2 kg increase in cow weight for every kg increase in weaning weight. In this model for each kg increase in weaning weight a corresponding increase of 1.5 kg was added to the mean cow weight.

There is no direct evidence reported in the literature on the genetic correlation between weaning weight and milk yield of beef cows. Extrapolation from studies on sheep and dairy cattle would suggest that for every kg increase in weaning weight a corresponding increase of 0.10-0.26 kg of milk yield per day (Barlow 1978). Diaz et al. (1992) recently reported the relationship between milk expected progeny difference of polled Hereford sires and actual milk production of their crossbred daughters. Extrapolation from this study would suggest that for one kg increase in weaning weight a corresponding increase of 0.10 kg of milk per day can be expected. In this model, for each kg increase in weaning weight a corresponding increase of 0.14 kg of milk was added to the mean daily milk yield.

Calf characteristics. Birth weight of female calves was calculated as 6% of mature cow weight. Birth weight of male calves was assumed to be 6.6% above that of female

calves (Wilton et al. 1974). The average birth weight (31 kg) was calculated as the mean birth weights of the male and female calves.

Feed requirements of the cow-calf pair. The daily feed requirements in terms of dry matter intake were determined for the beef cows and their nursing calves. The lactation curve of milk production was taken into consideration in calculating feed dry matter intake of cows and calves. Average daily milk yield per week was simulated using the equation $Y_n = A^*Be^{-cn}$ derived by Wood (1969) to describe a lactation curve where Y_n is average daily milk yield in the nth week and A, B and c are constants. The lactation curve (Figure 2) was simulated for a period of 32 weeks with the maximum milk yield occurring at about week 6. This simulated lactation curve closely resembled the curve simulated by Baker et al. (1976) in their milk and forage intake study. The purpose of simulating the lactation curve was two-fold. First, daily feed requirements of dams during the lactation period could be more accurately calculated. Secondly, calf forage dry matter intake relative to availability of milk from its dam could be determined.

Cow feed requirements - Daily dry matter requirements of the cow was calculated using the Net Energy System described by Lofgreen and Garrett (1968). This system makes it possible to calculate feed requirements separately for maintenance, gain, lactation and pregnancy. Net energy requirements for each of these components were calculated by basic formulae obtained from N.A.S.-N.R.C. (1984) and Wilton et al. (1974) and were

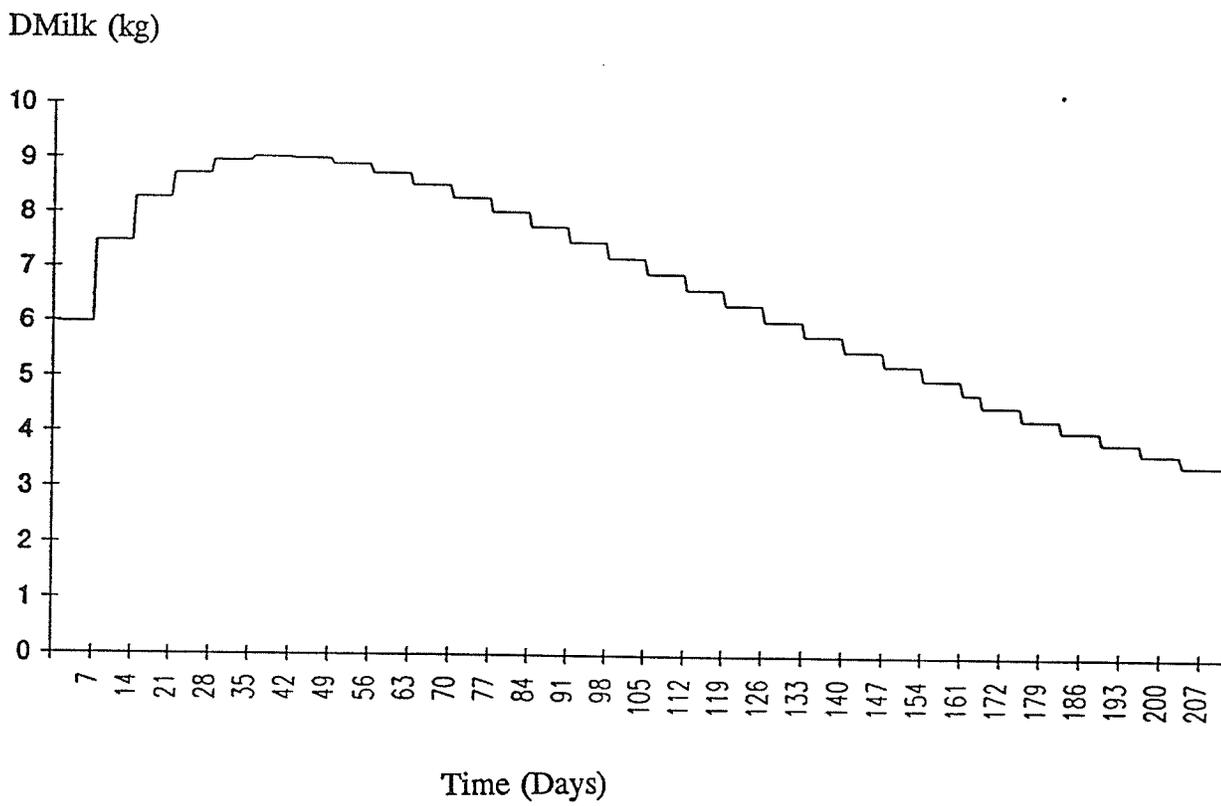


Figure. 2. Plot of simulated milk yield.

adapted for computer use for simulation of the biological inputs. Daily requirements of the different periods within each year cycle were calculated using the following expressions. Daily intake of forage dry matter for maintenance of cows (**FIMD**) was calculated from the formula:

$$\text{FIMD} = \text{NEM}/\text{NEMF} \quad (11)$$

In this equation **NEM** is net energy required for maintenance (Mcal d^{-1}) and is $0.077 W^{.75}$, with **W** representing weighted average cow weight and **NEMF** is energy density of forage ($\text{Mcal NE}_M \text{ kg}^{-1}$).

Daily intake of forage dry matter for gain of cows (**FIGD**) is calculated using the following formula:

$$\text{FIGD} = \text{NEG}/\text{NEGF} \quad (12)$$

NEG is net energy required for gain (Mcal d^{-1}) and is $[(0.05603 \text{ WG}) + 0.01265 (\text{WG})^2] W^{.75}$ where, **WG** is weight gain of cows and **W** is weighted average cow weight and **NEGF** is energy density of forage ($\text{Mcal NE}_G \text{ kg}^{-1}$).

Daily intake of forage dry matter to meet the lactation requirement of the dam (**FILD**) per kilogram milk production was calculated using the formula:

$$\text{FILD} = \text{NELD}/\text{NEMF} \quad (13)$$

and, NELD is $(0.1 \times \%FAT) \times 0.35.$, where %FAT was assumed to be 4% (Gleddie and Berg 1968).

Daily intake of forage dry matter for pregnancy requirement of cows (FIPD) was calculated using the formula:

$$FIPD = NEP/NEMF \quad (14)$$

NEP is $CBW \times (0.149 - 0.000407t) \exp(0.0583t - 0.000800t^2)$ where CBW is calf birth weight and t is day of pregnancy.

Calf feed requirements. The relative importance of milk and forage intake in the daily diet requirements of nursing calves was taken into consideration. To do this the relationship between availability of milk (quantity of milk dry matter) and forage dry matter intake needed to be specified. Such a relationship in beef cattle was investigated by Baker et al. (1976). They reported regression coefficients describing the influence of milk dry matter intake on forage dry matter intake. The lactation period was divided into six individual periods of 28 days each. The regression coefficients for each period were as follows:

| Period | 1 | 2 | 3 | 4 | 5 | 6 |
|-----------|-------|-------|-------|-------|-------|-------|
| Intercept | 35.6 | 26.7 | 24.1 | 17.9 | 22.8 | 22.4 |
| Slope | -3.11 | -2.12 | -2.19 | -1.71 | -2.21 | -2.60 |

(15)

where, the y axis for these equations represents grams of forage organic matter intake per kilogram live weight and the x axis represents grams of milk organic matter intake per kilogram live weight.

Recently Fox et al. (1988) used these coefficients to predict directly the forage dry matter intake of nursing calves. The formulae presented by Fox et al. (1988) were adapted to calculate daily forage dry matter consumption of a calf (**CifFI**) when the daily milk dry matter consumption of a calf (**CifMI**) was known. **CifMI** was assumed to be 12% of average daily milk yield. **CifFI** consumption was calculated using the following formula:

$$\text{CifFI} = (\text{IM} - (\text{BF} \times \text{CifMI}) / (\text{WW})) * \text{F} \quad (16)$$

where **IM** and **BF** are the intercept and regression coefficients, respectively, for each period shown above. **F** is a conversion factor needed to convert forage organic matter to forage dry matter (1.22).

Chronology of Events Through the 365 Day Cow-Calf Cycle

The cow-calf operation was described such that the yearly cycle begins on the 1st of March each year, which is the calving date for all calves. This is not what happens in practice - Spring calving is the usual procedure followed in Western Canada with the calving season extending from January to May. March 1 could be considered to be the

average calving date. The year was divided into 4 periods. These periods were of unequal lengths and were chosen to reflect physiological and/or management changes which were taking place. Calves are weaned at the end of the third period. Only the cows are present in the fourth period.

Period 1. This period starts on the 1st of March. During this period calves are dependent entirely on their dam's milk supply for their nourishment. Cow requirements during this period is the sum of requirements needed for maintenance, growth and lactation. This period ends on the 11th of April, i.e. 42 days from the beginning of the cycle.

Period 2. This period starts on the 12th of April and lasts for 42 days. Calves are dependent both on their dam's milk production and forage intake for their nourishment. This period ends on the 23rd of May, i.e. 84 days from the beginning of the cycle. Cow requirements during this period is the sum of the requirements needed for maintenance, growth and lactation, and calf requirements for forage intake are added to this.

Period 3. This period begins on the 24th of May and ends on the 28th of September (128 days). During this period calves are dependent on forage and milk supply from their dams. Calves are weaned at the end of this period. Day 85 marks the beginning of pregnancy of the cows. The feed requirements of the cow is the sum of maintenance, growth, lactation, and pregnancy requirements and the calf's requirements for forage

added onto this. The end of this period marks the end of lactation for the year.

Period 4. This period begins on the 29th of September and lasts 153 days. The requirement for this period is the sum of maintenance, growth and pregnancy requirements. Cows are 282 days in pregnancy at the end of this period (28th February) and the parturition on the 1st of March marks the beginning of a new year.

Economic Considerations

The main biological input in this study was feed requirement of cows and their nursing calves. It was assumed that the forage requirement was met entirely by feeding alfalfa brome-hay. In actual practice the cows and calves would be on pasture from late May to September. Simulation of pasture productivity, however, would introduce complexity beyond the scope of this study. The present simulation corresponds to a year-round drylot management regime where harvested forages are fed to cows and calves. Feed requirements were calculated in terms of dry matter intake and were converted to an as-fed basis.

The economic interpretation was entirely based on cost of purchasing the forage to meet feed requirements of the cow-calf pair and monetary benefits or returns obtained through the sale of weaned calves. All prices paid for costs and benefits were based on a 5 year average (1984-1988) obtained from the Manitoba Department of Agriculture (Janet Honey, personal communication). The average price of alfalfa brome-hay was calculated to be \$59.00 per tonne. The average price paid for weaned calves was \$2.00

kg⁻¹. Yearly net benefits per cow per year was calculated as the difference between the costs of feed (hay) to the cow-calf pair and the benefits obtained from selling weaned calves.

Partial Efficiency

Partial efficiency was defined as changes in the bioeconomic input output system to a unit increase of the direct or maternal component of weaning weight. As discussed earlier, the direct and maternal components of weaning weight are genetically correlated. Knowledge of the efficiency of one component independent of the influence of the other component should provide valuable information on the contributions of individual components to bioeconomic efficiency.

Describing Gene-Flow in a Population

When generations overlap, genetic contributions made by different age and sex groups of animals is best described using a gene-flow approach. This passage of genes through a population can be described in mathematical form by the application of matrix algebra (Hill 1974). To illustrate, a hypothetical example of a beef cattle population will be used. Hill (1974) and, Mueller and James (1985) used similar hypothetical examples to illustrate gene-flow in a pig population.

Gene-flow for a hypothetical purebred (Nucleus) population is described first. Assume for this example that only bulls of one age group are used for mating in each breeding season. These bulls are two years old when they have their progeny. Cows

of two age groups are allowed to reproduce each breeding season such that they are two and three years old when their progeny are born. In other words beef calves born at a certain time period (t) would on average obtain one half of their genes from bulls aged two years, one quarter from cows aged two years and another quarter from cows aged three years.

Paternally and maternally derived genes entering the population for any age group (i) at any time period (t) will now be developed (Hill 1974). In a population where males and females of different age groups interbreed, let $m(i,t)$ and $f(i,t)$ be the proportion of genes in males and females of age i and time period t . The proportion of genes in males of age 0 at time t for this hypothetical example is then:

$$m(0,t) = 0.5m(2,t) + 0.25f(2,t) + 0.25f(3,t) \quad (17)$$

The paternally derived genes which constitute one-half of the total genetic makeup is derived from males two units of age. The remaining portion of genes which are maternally derived are contributed from females of 2 and 3 age units. The source of genes in males which are one and two units of age can be described as:

$$m(1,t) = m(0,t-1) \text{ and } m(2,t) = m(1,t-1) \quad (18)$$

Males of age 1 unit derive their genes from males of age 0 units from the previous time period ($t-1$), and likewise males of age 2 units derive their genes from males of age 1

unit from the preceding time period. The genetic structure of the female population can also be described using the same logic as that for the male population. The origin of genes for females of age 0 is:

$$f(0,t) = 0.5m(2,t) + 0.25f(2,t) + 0.25f(3,t) \quad (19)$$

The source of genes for older females in the population is then:

$$f(1,t) = f(0,t-1), f(2,t) = f(1,t-1) \text{ and } f(3,t) = f(2,t-1) \quad (20)$$

These equations completely define one time period in terms of the previous time period. The passage of genes through the age-sex group can thus be followed through an iterative process. These time sequence events can be easily put in matrix form.

$$V_t = P V_{(t-1)} \quad (21)$$

$$\begin{bmatrix} m_{1(t)} \\ m_{2(t)} \\ f_{1(t)} \\ f_{2(t)} \\ f_{3(t)} \end{bmatrix} = \begin{bmatrix} P_{1m} & P_{2m} & P_{1f} & P_{2f} & P_{3f} \\ 1 & 0 & 0 & 0 & 0 \\ P_{1m} & P_{2m} & P_{1f} & P_{2f} & P_{3f} \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} m_{1(t-1)} \\ m_{2(t-1)} \\ f_{1(t-1)} \\ f_{2(t-1)} \\ f_{3(t-1)} \end{bmatrix}$$

The matrix P is a modified Leslie matrix. The matrix has partitions which describes the alternative pathways of genes between the male and female sexes of the population. The first row within each submatrix describes the proportion of genes contributed by each age-sex group. The remaining rows account for ageing in the population. This "ageing", as mentioned above, simply describes the passage of individuals from one age group into the next as time passes. This matrix which describes the genetic structure of the population can be used to project the passage of genes of individuals in the next time unit. It is assumed that this structure does not change.

Consider that in this hypothetical population only bull calves are selected and thus the source of genetic change is only from the male population. This may be observed in a vector (V_t) which describes the passage of genes from the selected male population deriving from bulls of age 1 time unit (1 year) at the start of the selection programme at time 0 to subsequent time units (years) in the future.

$$P V_{(t-1)} = P V_{(t)} \quad (22)$$

and,

$$\begin{bmatrix} 0 & 0.50 & 0 & 0.25 & 0.25 \\ 1.00 & 0 & 0 & 0 & 0 \\ 0 & 0.50 & 0 & 0.25 & 0.25 \\ 0 & 0 & 1.00 & 0 & 0 \\ 0 & 0 & 0 & 1.00 & 0 \end{bmatrix} \begin{bmatrix} 1.00 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} = \begin{bmatrix} 0 \\ 1.00 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

The distribution of genes derived from the original selected males into the various age-sex categories in the population can be updated for each successive time interval. Suppose we would like to know the proportion of genes present in the population from a single cycle of selection on this source group in 20 years, P then would be multiplied by the updated vector of each of the 20 time units (years). Due to overlapping generations, the proportion of genes from the initial source group fluctuates in the initial periods (years) but eventually stabilizes (Table 1, Figure 3). To predict response to selection for weaning weight, assuming for the moment that it is a simple trait with no maternal component, genetic parameters for this trait need to be specified. Heritability of weaning weight can be assumed to be 0.313 (Trus and Wilton 1988). A selection intensity of 1.45 was used for this particular example. The phenotypic standard deviation for weaning weight was 28.75 kg. Using these parameters the genetic selection differential for weaning weight (ΔG) was calculated to be 13.05 kg. Prediction of response (R) in this situation is straightforward.

$$R_{t(i)} = P V_{(i)} \Delta G \quad (23)$$

$$= \begin{bmatrix} 0 & 0.50 & 0 & 0.25 & 0.25 \\ 1.00 & 0 & 0 & 0 & 0 \\ 0 & 0.50 & 0 & 0.25 & 0.25 \\ 0 & 0 & 0 & 1.00 & 0 \\ 0 & 0 & 0 & 0 & 1.00 \end{bmatrix} \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \begin{bmatrix} 13.05 \end{bmatrix}$$

Table 1. Proportion of genes derived from yearling males selected at time 0, over 20 years

| Year | Males |
|------|----------|
| 0 | 1.000000 |
| 1 | 0.000000 |
| 2 | 0.500000 |
| 3 | 0.000000 |
| 4 | 0.375000 |
| 5 | 0.125000 |
| 6 | 0.281250 |
| 7 | 0.187500 |
| 8 | 0.242188 |
| 9 | 0.210938 |
| 10 | 0.228516 |
| 11 | 0.218750 |
| 12 | 0.224121 |
| 13 | 0.221191 |
| 14 | 0.222778 |
| 15 | 0.221924 |
| 16 | 0.222382 |
| 17 | 0.222137 |
| 18 | 0.222267 |
| 19 | 0.222198 |
| 20 | 0.222235 |

PROPORTION OF GENES

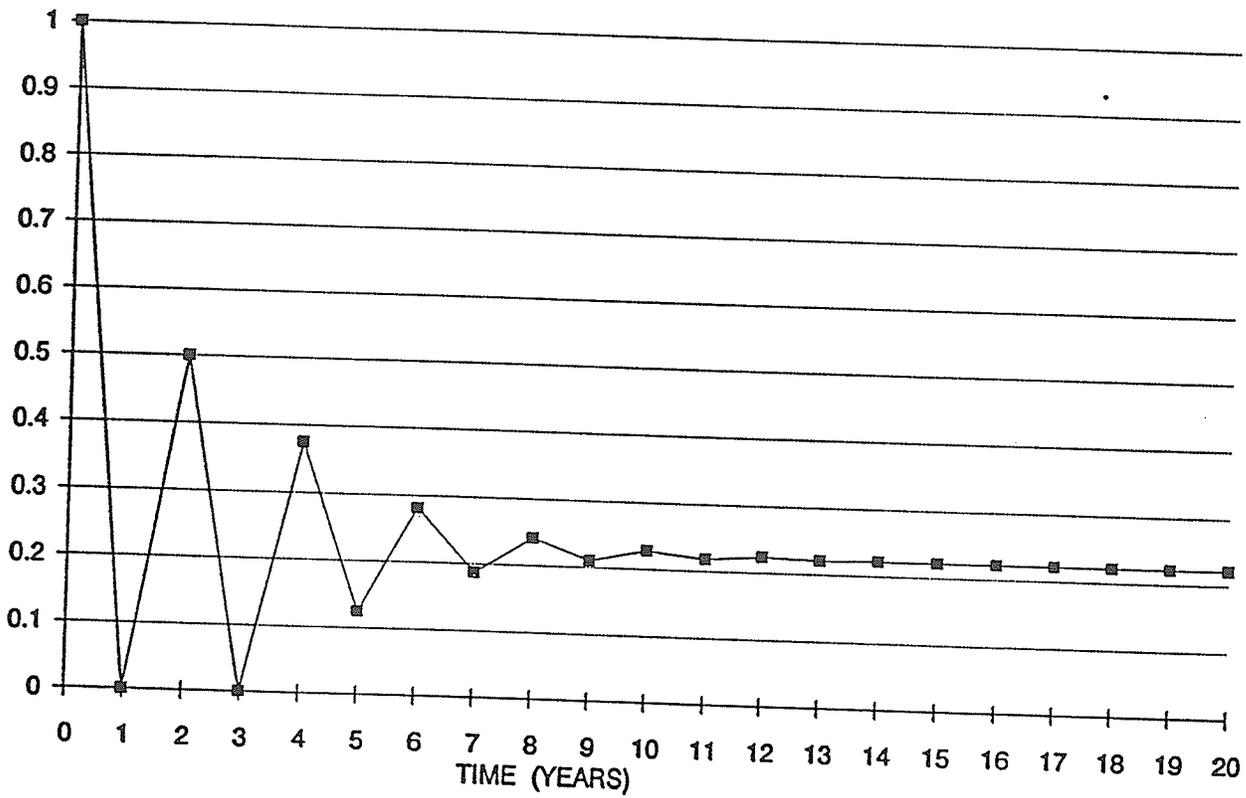


Figure 3. Proportion of genes from males selected in time zero, over 20 years.

R is response to selection for time unit 1. Response to selection covering an evaluation period of 20 years is illustrated in Figure 4.

Weaning weight is not a simple trait, however, and is composed of direct and maternal components. Therefore additional vectors ($V_{P:D}$) and ($V_{P:M}$) are needed to describe the proportion of genes contributed by each age-sex group for the individual components (Mueller and James 1985).

Both males and females contribute equally to the direct component of weaning weight. For this population then, the proportion of genes contributed by each age-sex group to the current calf crop may be described by the vector ($V_{P:D}$) as follows:

$$V_{P:D} = \begin{array}{|c} 0.00 \\ 0.50 \\ 0.00 \\ 0.25 \\ 0.25 \end{array}$$

As maternal effects are sex limited and expressed only in the reproducing females, another vector is needed to account for the maternal contribution made by females of different age groups. Thus for the maternal component, the maternal effect contributed by female age groups to the current calf crop may be described by the vector ($V_{P:M}$) as follows:

Response (kg)

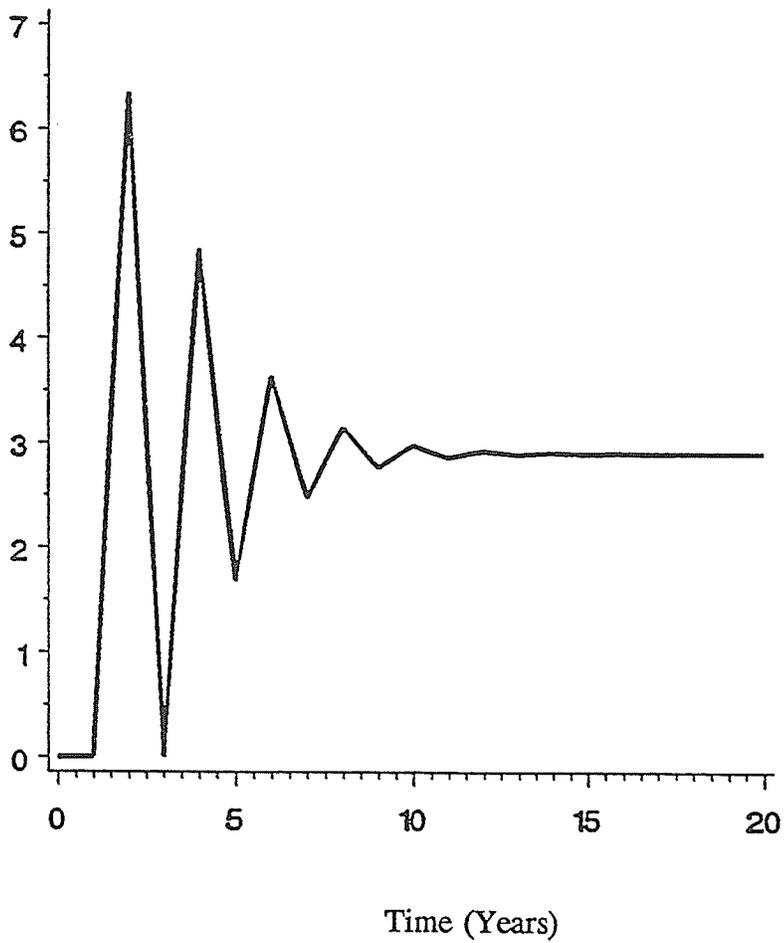


Figure 4. Response from a single cycle of selection in the nucleus sector.

$$V_{P:M} = \begin{array}{|c|} \hline 0.00 \\ \hline 0.00 \\ \hline 0.00 \\ \hline 0.50 \\ \hline 0.50 \\ \hline \end{array}$$

In other words half of the maternal effects are attributed to females of age 2 years and the remaining half to females of age 3 years. To calculate the individual growth and maternal responses, the heritabilities for the growth and maternal components and the genetic correlation between the components need to be specified. Heritabilities of the growth and maternal components were assumed to be 0.36 and 0.22, respectively, and the genetic correlation between these components was assumed to be -0.36 (Trus and Wilton 1988). Using these parameters the genetic selection differentials for direct (ΔG_D) and maternal (ΔG_M) effects were calculated to be 12.69 and 0.36 kg, respectively. Thus response to selection at time unit 1 (year 1) after a single cycle of selection at the start of the programme ($t=0$) for direct effects is $P V_{(t-1)} \Delta G_D V_{P:D}$, and for maternal effects is $P V_{(t-1)} \Delta G_M V_{P:M}$. Total response ΔG_{WW} is simply the sum of the individual direct and maternal responses.

The complete sequence of events for time unit 1 is described with the help of a flow diagram in Figure 5. Phenotypic (ΔG_{WW}), direct (ΔG_{WWD}) and maternal (ΔG_{WWM}) responses computed following the steps in the flow diagram are shown for a 20 time unit (year) period in Table 2 and Figure 6.

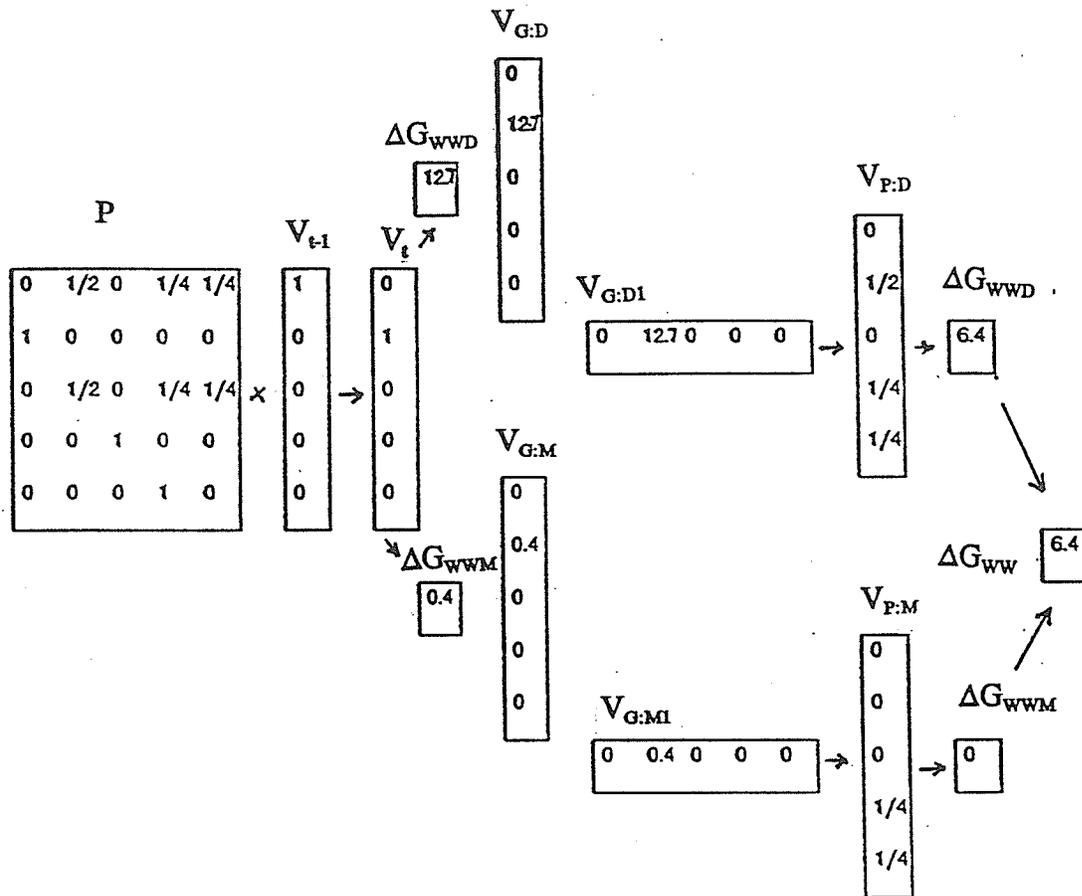


Figure 5. Flow diagram of direct (ΔG_{wwd}), maternal (ΔG_{wwm}) and total (ΔG_{ww}) responses.

Table 2. Total (ΔG_{ww}), direct (ΔG_{wwD}) and maternal (ΔG_{wwM}) responses in weaning weight

| Year | ΔG_{ww} | ΔG_{wwD} | ΔG_{wwM} |
|------|-----------------|------------------|------------------|
| 0 | 0.00000 | 0.00000 | 0.0000000 |
| 1 | 0.00000 | 0.00000 | 0.0000000 |
| 2 | 6.34700 | 6.34700 | 0.0000000 |
| 3 | 0.00000 | 0.00000 | 0.0000000 |
| 4 | 4.85057 | 4.76025 | 0.0903250 |
| 5 | 1.67707 | 1.58675 | 0.0903250 |
| 6 | 3.63793 | 3.57019 | 0.0677437 |
| 7 | 2.47045 | 2.38012 | 0.0903250 |
| 8 | 3.14772 | 3.07433 | 0.0733891 |
| 9 | 2.76232 | 2.67764 | 0.0846797 |
| 10 | 2.97840 | 2.90078 | 0.0776230 |
| 11 | 2.85867 | 2.77681 | 0.0818570 |
| 12 | 2.92438 | 2.84499 | 0.0793872 |
| 13 | 2.88860 | 2.80780 | 0.0807985 |
| 14 | 2.90795 | 2.82795 | 0.0800047 |
| 15 | 2.89755 | 2.81710 | 0.0804457 |
| 16 | 2.90312 | 2.82291 | 0.0802031 |
| 17 | 2.90015 | 2.81981 | 0.0803354 |
| 18 | 2.90172 | 2.82146 | 0.0802638 |
| 19 | 2.90089 | 2.82059 | 0.0803024 |
| 20 | 2.90133 | 2.82105 | 0.0802817 |

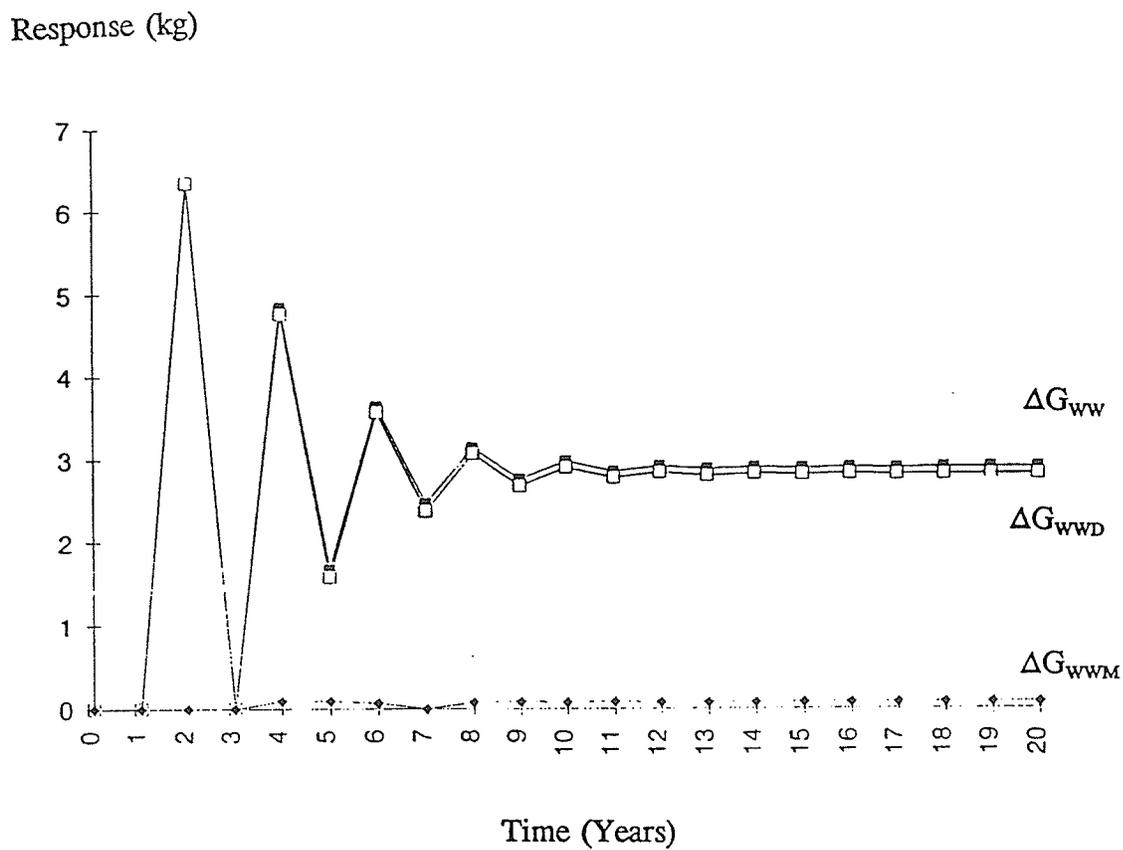


Figure 6. Total (ΔG_{ww}), direct (ΔG_{wwd}) and maternal (ΔG_{wwm}) responses after a single cycle of selection in the nucleus sector.

Gene-flow in hierarchial populations. The gene-flow concept may be expanded to completely accommodate the hierarchial structure of a beef cattle population. This can be done by expanding the P matrix developed previously to include the commercial sector of the population. For the purpose of illustration here, let us assume that sires from the nucleus sector are bred to dams in the nucleus herds when they are 1 and 2 years of age. The dams in these herds have their calves when they are two and three years of age. A new P matrix can thus be constructed which fully accounts for the age and sex groups within each strata of the population.

$$P = \begin{bmatrix} 0 & 0.50 & 0 & 0 & 0.25 & 0.25 & 0 & 0 & 0 \\ 1.00 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1.00 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.50 & 0 & 0 & 0.25 & 0.25 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1.00 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1.00 & 0 & 0 & 0 & 0 \\ 0 & 0.25 & 0.25 & 0 & 0 & 0 & 0 & 0.25 & 0.25 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1.00 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1.00 & 0 \end{bmatrix}$$

The first three rows describes the flow of male genes in the nucleus, the second three rows describes the flow of female genes in the nucleus. The last three rows describe the flow of female genes in the commercial population. Total (ΔG_{ww}), direct (ΔG_{wwd}) and maternal (ΔG_{wwm}) responses are computed for this structured population using the same concepts as described for the more simply-structured population earlier.

Describing a Hypothetical Structured Population

As discussed in the review of literature, beef cattle population appears to have a hierarchial structure. Information on this hierarchy for the Manitoba beef cattle population was obtained from a survey carried out by the Manitoba Department of Agriculture (1986). The information obtained from the analysis of the survey data provided some knowledge of the structure and breeding activity of the population. The beef cattle population in the province has essentially two major sectors - nucleus herds and commercial herds (Figure 7). The nucleus sector is very much a closed population as more than 95% of purebred producers bought their breeding bulls from other purebred producers. However, breeding bulls used in the commercial population were mostly (72%) bought from the nucleus sector. The remaining 28% of the breeding bulls came from other commercial herds. This information and other relevant information obtained from the literature were used to define the breeding and gene flow activity in the hypothetical population.

Bulls in the nucleus sector. In the nucleus sector only, it was assumed that bulls of one

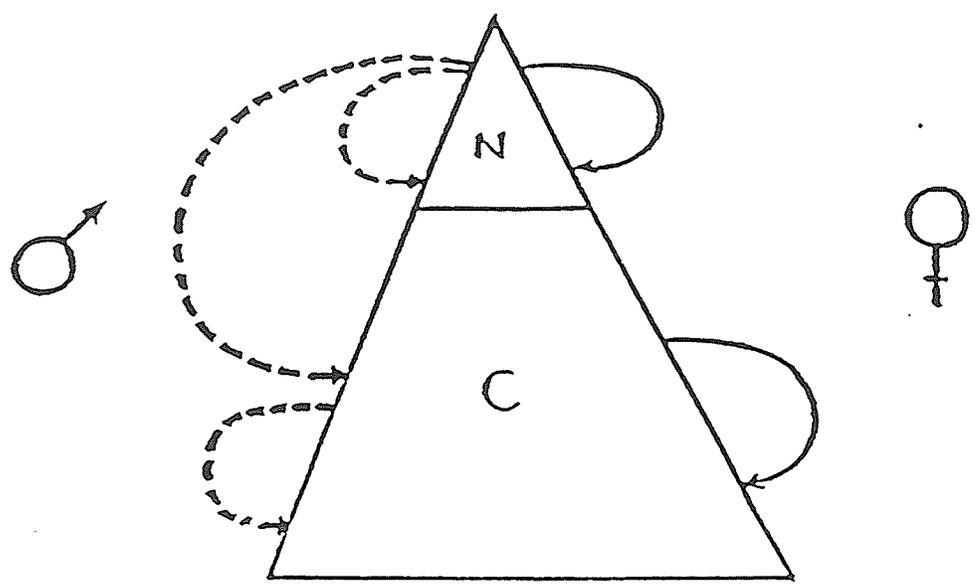


Figure 7. Gene-flow in a two-tier population structure.

or two years of age were used for breeding such that the progeny were born when the bulls are 2 and 3 years old. This assumption was made based on reports that indicate sires used for breeding range between 2 and 4 years of age (Mrode 1988).

Nucleus bulls to mate commercial cows. Bulls used in the commercial population are assumed to have their progeny when 2, 3 and 4 years of age. As 72% of the bulls used in the commercial population are bought from the purebred producers, the total proportion of paternally-derived genes from the nucleus source is:

$$0.72 \times 0.50 = 0.36 \quad (24)$$

It is assumed that each age group contributes an equal proportion of genes to the progeny crop.

Commercial bulls to mate commercial cows. The remaining 28% of the bulls used in the commercial sector were obtained from within the commercial population. It was assumed that bulls of 2 and 3 years of age contributed equally to the progeny crop. Mrode (1988) reported that the average age of sires in beef cattle populations range from 2 to 4 years. Therefore the total proportion of paternally derived genes from the commercial source is:

$$0.28 \times 0.5 = 0.14 \quad (25)$$

Commercial cows. The age distribution and proportion of genes contributed by each age group was assumed to be similar to that of the nucleus cow population. All the pertinent information just described was used to construct a gene flow matrix that described the genetic structure of the population and accounted for passage of genes from the source group through the various strata of the population (Figure 8).

Parameters Used in the Prediction of Response to Selection

Parameters used for the prediction of response to selection were exactly the same as that used in the Base Model for the more simply-structured population discussed earlier. The heritability assumed for weaning weight was 0.30, the heritability for the growth component was 0.40 and the heritability for the maternal component was 0.20. The genetic correlation between the growth and maternal component was -0.40. The phenotypic standard deviation for weaning weight was 29 kg.

Simulation of Response to Selection

Using the hypothetical gene flow matrix for the beef cattle population in Manitoba and the above parameters, the mean direct and maternal breeding values of each age and sex group were computed. From these breeding values phenotypic changes in weaning weight of commercial calves were determined. Response was simulated for a period of 20 years based on a single cycle of selection at the beginning of the programme at year 0. Correlated responses in cow size and milking ability and the set of traits used to calculate costs and returns were calculated for each year as well.

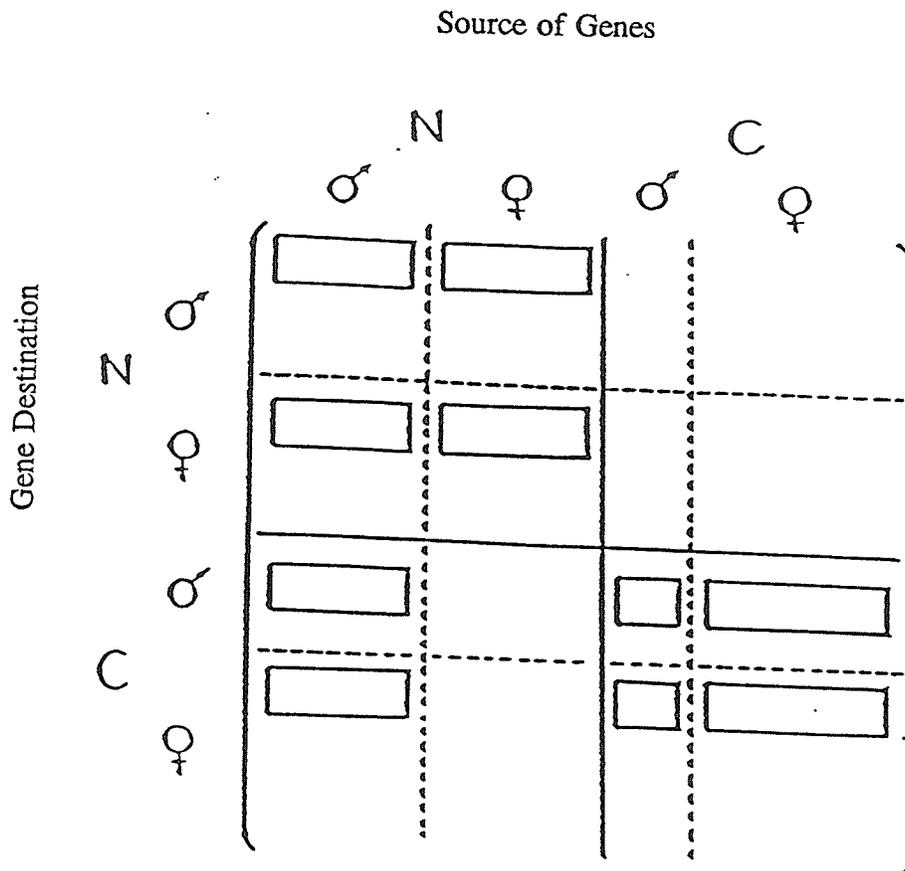


Figure 8. Schematic of matrix (P) describing gene-flow in the Manitoba beef cattle population.

Biological and Economic Considerations

The biological considerations were similar to that used earlier for the uniform rate of response model (Base Model). The economic considerations are also the same as those used earlier for the uniform rate of response model (Base Model). Net discounted monetary returns were calculated using a 4% discount rate.

RESULTS AND DISCUSSION

Base Model

Phenotypic response to selection. Changes in the phenotypic value as well as changes in the magnitude of the direct and maternal components of weaning weight were computed. Phenotypic response was computed as the sum of the direct and maternal responses. Response for the Base Model was predicted by assuming a uniform rate of response (Rendel and Robertson, 1950), and is shown in Table 3. The phenotypic response (ΔG_{ww}) was 2.57 kg yr⁻¹. The direct response (ΔG_{wwD}) indicated a gain of 2.67 kg yr⁻¹, while the maternal response (ΔG_{wwM}) recorded a loss of 0.10 kg yr⁻¹. The phenotypic response (ΔG_{ww}) was lower than the direct response (ΔG_{wwD}) due to a loss of 0.10 kg yr⁻¹ for the maternal response (ΔG_{wwM}).

For the last few years Agriculture Canada, through the Canadian Beef Sire Evaluation Program, provides estimates of breeding values in the form of Expected Progeny Difference (EPDs), twice annually. In a recent publication (Agriculture Canada 1993), genetic trends for direct and maternal components of weaning weight were reported for various breeds. Direct and maternal genetic trends were plotted for weaning weight relative to 1976 breed averages. The trend analysis for the Hereford breed indicated an average genetic gain of 0.62 kg yr⁻¹ for the direct genetic component, and a average genetic gain of 0.34 kg yr⁻¹ for the maternal genetic component. For the Angus breed, a direct genetic gain of 0.2 kg yr⁻¹, and a maternal genetic loss of 0.11 kg yr⁻¹ was

Table 3. Response to selection with base set of assumed genetic parameters ($h^2_D=0.4$, $h^2_M=0.2$, $r_{G:WWD,WWM}=-0.4$)

| Component | Definition | Units | Value |
|------------------|--|------------|--------|
| ΔG_{WWD} | Genetic gain of the direct component | σ_P | 0.34 |
| ΔG_{WWM} | Genetic gain of the maternal component | σ_P | -0.013 |
| ΔG_{WW} | Total genetic gain | σ_P | 0.33 |
| ΔG_{WWD} | Direct genetic response | kg | 2.67 |
| ΔG_{WWM} | Maternal genetic response | kg | -0.10 |
| ΔG_{WW} | Total genetic response | kg | 2.57 |

reported. Variation in the genetic trend for these two breeds may be due to breed differences in genetic parameters for weaning weight. However, the true underlying reason is not known. There was a need, therefore, to test the sensitivity of the model to variations in the genetic parameters of weaning weight.

Sensitivity of Response to Selection

In this section response was simulated for a range of genetic parameters of weaning weight. This was considered important given the range of $r_{G:WWD,WWM}$ reported in the literature. Sensitivity of response to these range of possibilities should provide valuable information in designing selection programmes. Sensitivity of response to the range of genetic correlations was simulated for various heritability values of the direct and maternal components of weaning weight.

Heritability of direct component equals heritability of maternal component (Table 4, Figure 9). For $r_{G:WWD,WWM} = -0.4$, 89% of the total phenotypic response (ΔG_{WW}) was attributed to the direct component. In the absence of a genetic correlation between the direct and maternal components ($r_{G:WWD,WWM} = 0$), response due to the direct component (ΔG_{WWD}) dropped to 67%. With a positive value for $r_{G:WWD,WWM}$, the percentage of contribution of the direct component further decreased (57% for $r_{G:WWD,WWM} = 0.4$). However, the direct response (ΔG_{WWD}) was still greater than the maternal response.

Table 4. Sensitivity of response to selection

| h^2_D | h^2_M | $r_{G:WWD,WWM}$ | ΔG_{WWD} | ΔG_{WWM} | ΔG_{WW} | % G_{WWD} | % G_{WWM} |
|---------|---------|-----------------|------------------|------------------|-----------------|-------------|-------------|
| 0.2 | 0.2 | -0.4 | 1.25 | 0.16 | 1.41 | 88.65 | 11.35 |
| | | -0.3 | 1.32 | 0.31 | 1.63 | 80.98 | 19.02 |
| | | -0.2 | 1.40 | 0.47 | 1.87 | 74.87 | 25.13 |
| | | -0.1 | 1.48 | 0.62 | 2.10 | 70.48 | 29.52 |
| | | 0.0 | 1.56 | 0.78 | 2.34 | 66.67 | 33.33 |
| | | 0.1 | 1.63 | 0.93 | 2.56 | 63.67 | 36.33 |
| | | 0.2 | 1.71 | 1.09 | 2.80 | 61.07 | 38.93 |
| | | 0.3 | 1.79 | 1.25 | 3.04 | 58.88 | 41.12 |
| | | 0.4 | 1.87 | 1.40 | 3.27 | 57.19 | 42.81 |
| | | 0.4 | 0.2 | -0.4 | 2.67 | -0.10 | 2.57 |
| -0.3 | 2.78 | | | 0.12 | 2.90 | 95.86 | 4.14 |
| -0.2 | 2.89 | | | 0.34 | 3.23 | 89.47 | 10.53 |
| -0.1 | 3.00 | | | 0.56 | 3.56 | 84.27 | 15.73 |
| 0.0 | 3.11 | | | 0.78 | 3.89 | 79.95 | 20.05 |
| 0.1 | 3.22 | | | 1.00 | 4.22 | 76.30 | 23.70 |
| 0.2 | 3.33 | | | 1.22 | 4.55 | 73.19 | 26.81 |
| 0.3 | 3.44 | | | 1.44 | 4.88 | 70.49 | 29.51 |
| 0.4 | 3.55 | | | 1.66 | 5.21 | 68.14 | 31.86 |
| 0.2 | 0.4 | | | -0.4 | 1.12 | 0.68 | 5.21 |
| | | -0.3 | 1.23 | 0.90 | 2.13 | 57.75 | 42.25 |
| | | -0.2 | 1.34 | 1.12 | 2.46 | 54.47 | 45.53 |
| | | -0.1 | 1.45 | 1.34 | 2.79 | 51.97 | 48.03 |
| | | 0.0 | 1.56 | 1.56 | 3.12 | 50.00 | 50.00 |
| | | 0.1 | 1.67 | 1.78 | 3.45 | 48.41 | 51.59 |
| | | 0.2 | 1.78 | 2.00 | 3.78 | 47.09 | 52.91 |
| | | 0.3 | 1.89 | 2.22 | 4.11 | 45.99 | 54.01 |
| | | 0.4 | 2.00 | 2.44 | 4.44 | 45.05 | 54.95 |

h^2_D Heritability of direct component.

h^2_M Heritability of maternal component.

$r_{G:WWD,WWM}$ Genetic correlation between direct and maternal components of weaning weight.

ΔG_{WWD} Direct genetic response in kg y^{-1} .

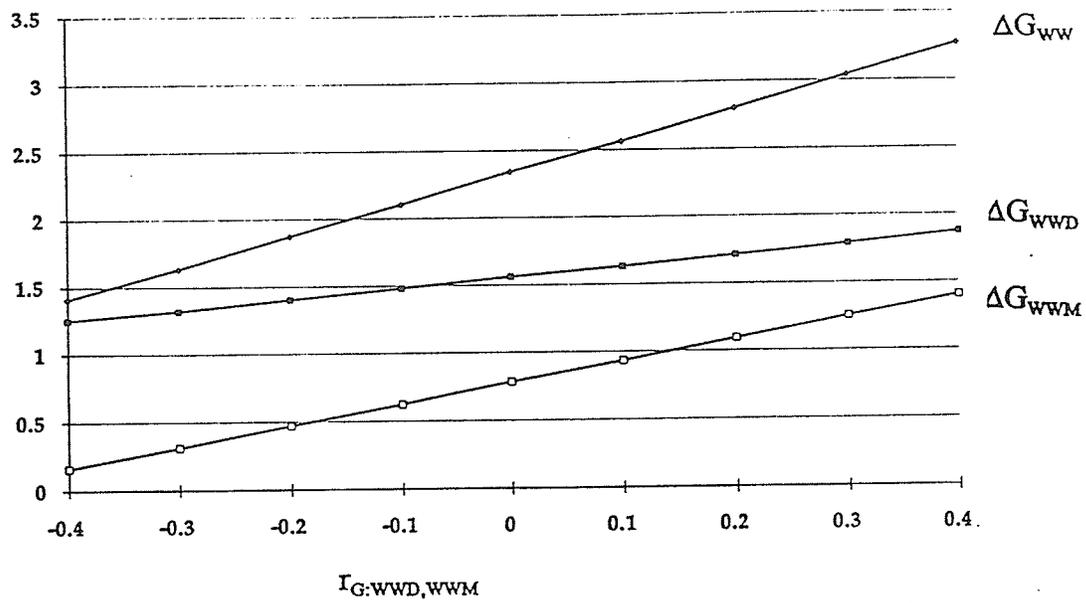
ΔG_{WWM} Maternal genetic response in kg y^{-1} .

ΔG_{WW} Total phenotypic response in kg y^{-1} .

% G_{WWD} Percent direct response relative to total phenotypic response.

% G_{WWM} Percent maternal response relative to total phenotypic response.

Response (kg)



Percent of phenotypic response

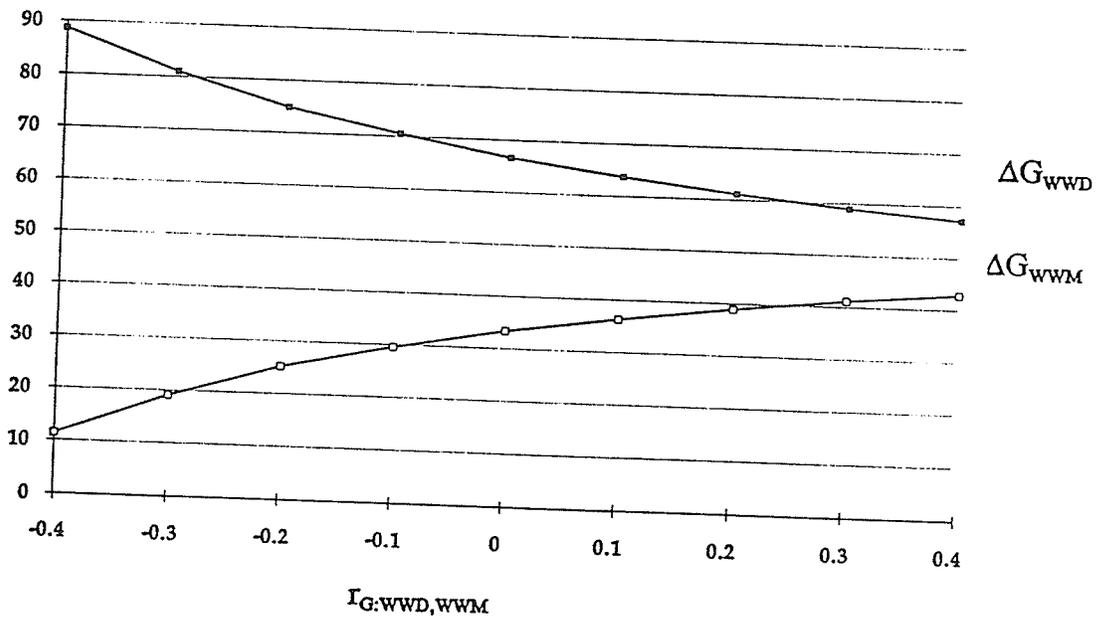


Figure 9. Sensitivity of response to selection: Heritability of direct component ($h^2_D=0.2$) equals heritability of maternal component ($h^2_M=0.2$).

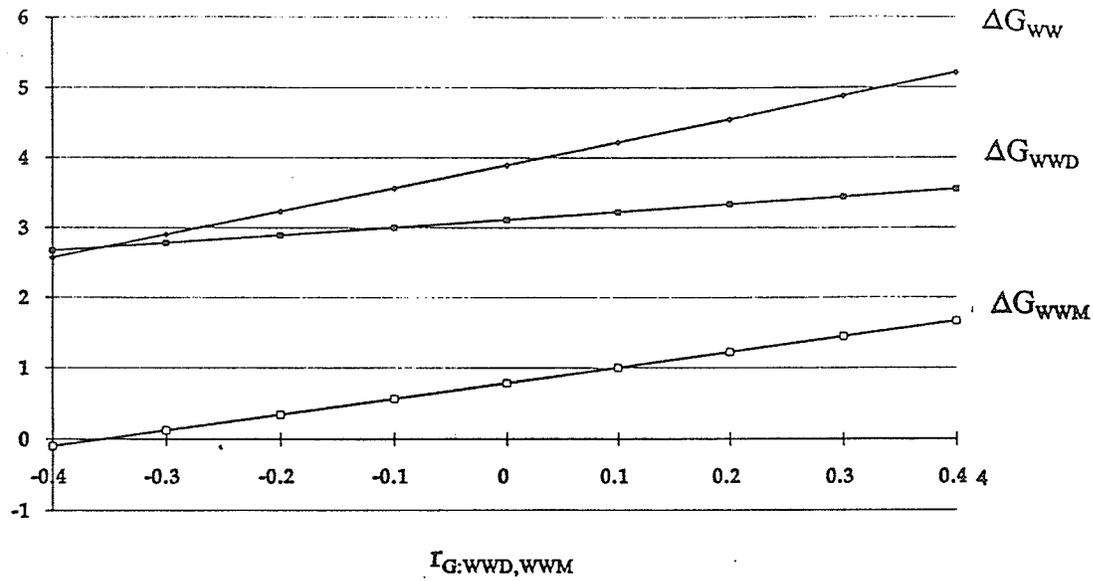
Heritability of direct component larger than heritability of maternal component (Table 4, Figure 10). For $r_{G:WWD,WWM} = -0.4$, there was a genetic loss in maternal response (ΔG_{WWM}) and amounted to 3.97%, the direct response (ΔG_{WWD}) therefore accounted for 100% of the total response (ΔG_{WW}) in weaning weight. As $r_{G:WWD,WWM}$ moved to zero, 80% of the phenotypic response (ΔG_{WW}) was attributed to the direct component. With a positive increase in $r_{G:WWD,WWM}$, phenotypic response (ΔG_{WW}) due to the direct component dropped to 68% of the total response, while the maternal response (ΔG_{WWM}) increased to 32% for $r_{G:WWD,WWM} = 0.4$.

Heritability of maternal component larger than heritability of direct component (Table 4, Figure 11). For $r_{G:WWD,WWM} = -0.4$, 62% of the total phenotypic response (ΔG_{WW}) was accounted by the direct component. However, for $r_{G:WWD,WWM} = 0$, the direct and maternal components contributed equally to total phenotypic response. For positive $r_{G:WWD,WWM}$ values, the maternal contribution was marginally greater than the direct component.

Across the range of $r_{G:WWD,WWM}$, the proportional contribution to ΔG_{WW} due to the direct response (ΔG_{WWD}) decreased as $r_{G:WWD,WWM}$ changed from negative to positive values. Maternal genetic response (ΔG_{WWM}) was highest when heritability of the maternal component was larger than heritability of the direct component. For all combinations of heritability values of the direct and maternal components of weaning weight, there was almost a linear increase in maternal response as $r_{G:WWD,WWM}$ changed from negative to positive values. Total phenotypic response (ΔG_{WW}) was greatest when

Response (kg)

59



Percent of phenotypic response

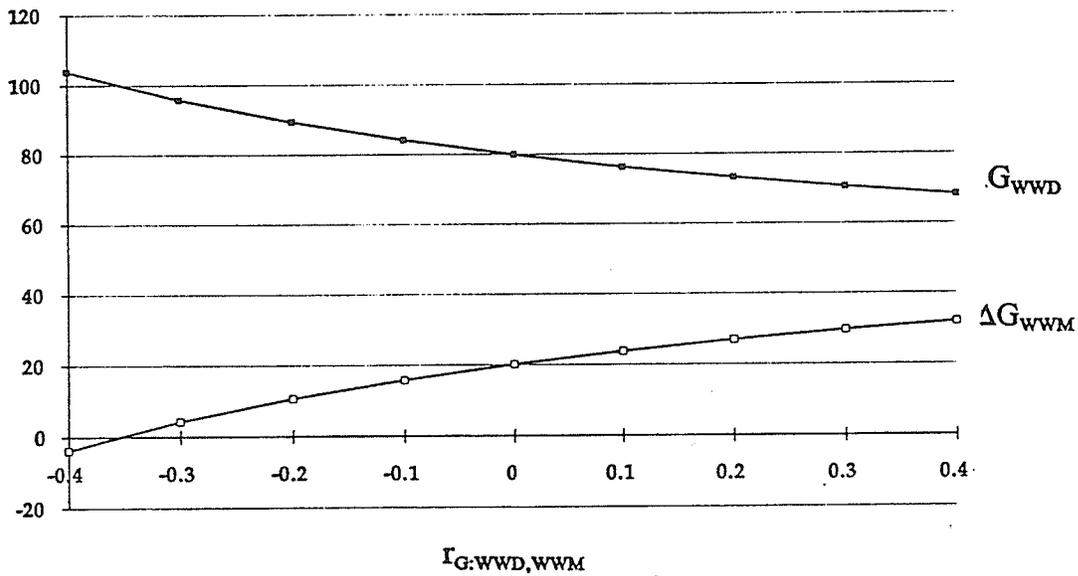
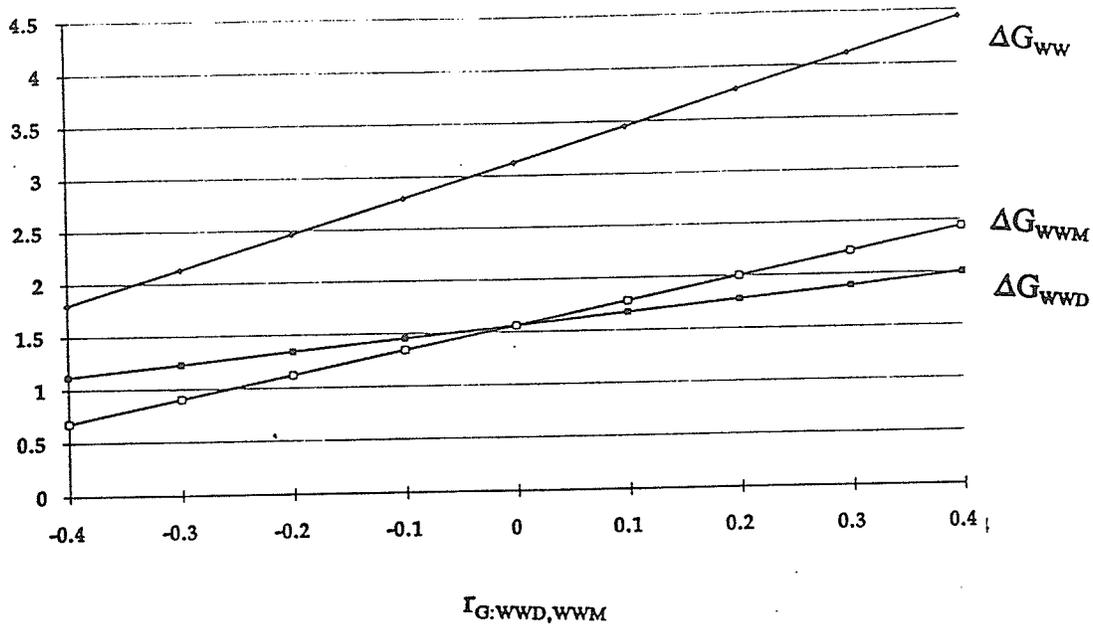


Figure 10. Sensitivity of response to selection: Heritability of direct component ($h^2_D=0.4$) larger than heritability of maternal component ($h^2_M=0.2$).



Percent of phenotypic response

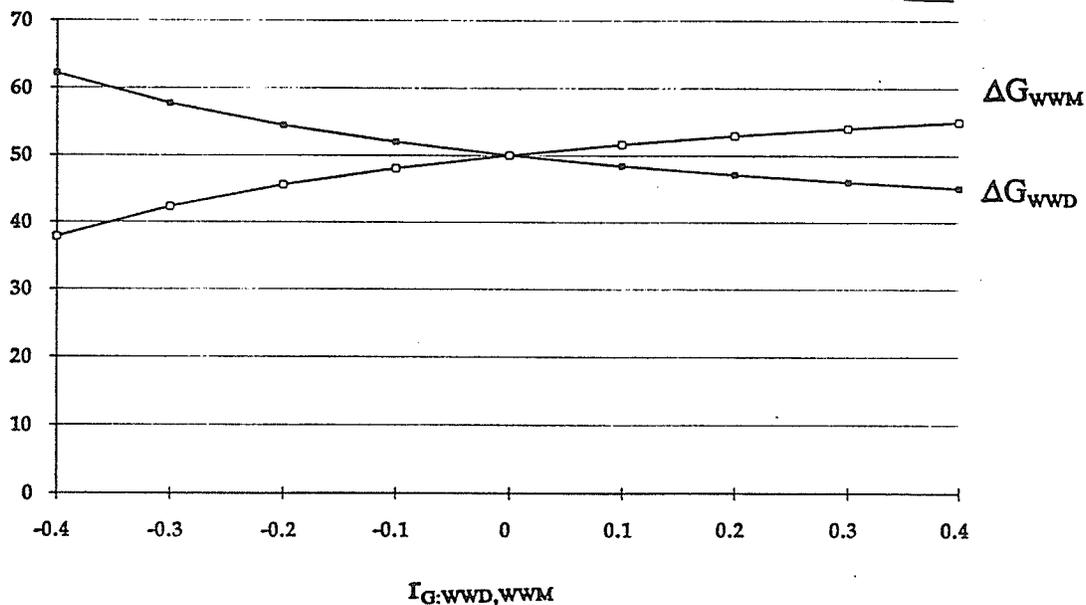


Figure 11. Sensitivity of response to selection: Heritability of maternal component ($h^2_M=0.4$) larger than heritability of direct component ($h^2_D=0.2$).

heritability of the direct component was larger than heritability of the maternal component. There was also a linear increase in phenotypic response (ΔG_{ww}) as the $r_{G:WWD,WWM}$ changed from negative to positive values.

Sensitivity of response to the range of $r_{G:WWD,WWM}$ highlight the potential consequences of the lack of knowledge of $r_{G:WWD,WWM}$ on response to selection programmes based on weaning weight. In general, phenotypic response (ΔG_{ww}) was highest for $r_{G:WWD,WWM}=0.4$. In contrast for $r_{G:WWD,WWM}=-0.4$, phenotypic response (ΔG_{ww}) was lowest. These simulations clearly indicate the detrimental effects of negative $r_{G:WWD,WWM}$ on total phenotypic response in weaning weight. Response predicted from this stimulation was based on the range of $r_{G:WWD,WWM}$ and heritability values reported in the literature based on designed experiments as well as field data analysis.

Correlated Changes in Biological Characteristics Due to Selection on Weaning Weight

The aim of this research was to examine the consequences of selecting for weaning weight on the bioeconomic efficiency of the beef cow-calf input-output system. Correlated changes in the bioeconomic characteristics of the beef cow-calf input-output system as a result of selection were computed. Reports in the literature are scanty on correlated changes in bioeconomic characteristics due to selection for weaning weight (Barlow 1978; Armstrong et al. 1990).

Changes in calf characteristics. Calf weaning weight (WW) increased by 2.57 kg which translates to an increase of 1.12% to the original mean used in the model (230 kg) (Table 5). This increase was due to an increase in the direct component of weaning weight as a result of selection for weaning weight and a decrease in the maternal component, with a net positive change. The total genetic gain was reduced by the genetic loss from the maternal component due to negative $r_{G:WWD, WWM}$.

Calf forage dry matter intake (CifFI) and calf milk dry matter intake (CifMI) were predicted directly from the regression coefficients obtained from the work of Baker et al. (1976). The pattern of response for CifFI and CifMI is illustrated in Figure 12. The jagged lines for CifFI are indicative of the individual regression coefficients used for each period to predict CifFI in relation to availability of CifMI and corresponding weight of calf. The original experimental data from which these coefficients were obtained also show a similar "up down" trend across the periods in terms of grams of forage dry matter intake per kg liveweight. In general, the pattern of response was similar in direction and magnitude to that reported by Fox et al. (1988) for medium frame size and comparable calf weaning weights and cow milk production. As a result of selection CifFI increased by 7.67 kg from the original mean of 402.99 kg, or increase of 1.92%. The increase in CifFI was due to the loss in CifMI as a result of reduction in milk yield. The additional food intake of 7.67 kg represents an efficiency of 3 kg of forage kg^{-1} gain in calf weaning weight.

Changes in cow characteristics. Cow weight (CowWt) increased by 4.01 kg which

Table 5. Changes in cow and calf characteristics due to selection for weaning weight

| Variable Name | Variable Definition | Mean or Base Value | Response kg per year |
|---------------|------------------------------------|--------------------|----------------------|
| WW | Calf weaning weight (kg) | 230 | 2.57 |
| CowWt | Cow weight (kg) | 470 | 4.01 |
| TMilk | Total milk yield (kg) | 1356.80 | -3.03 |
| ClfMI | Calf milk dry matter intake (kg) | 167.81 | -0.38 |
| ClfFI | Calf forage dry matter intake (kg) | 402.99 | 7.67 |
| CowFI | Cow forage dry matter intake (kg) | 2811.77 | 14.11 |
| Profit | Profit in dollars (\$ cow-calf) | 244.53 | 3.68 |

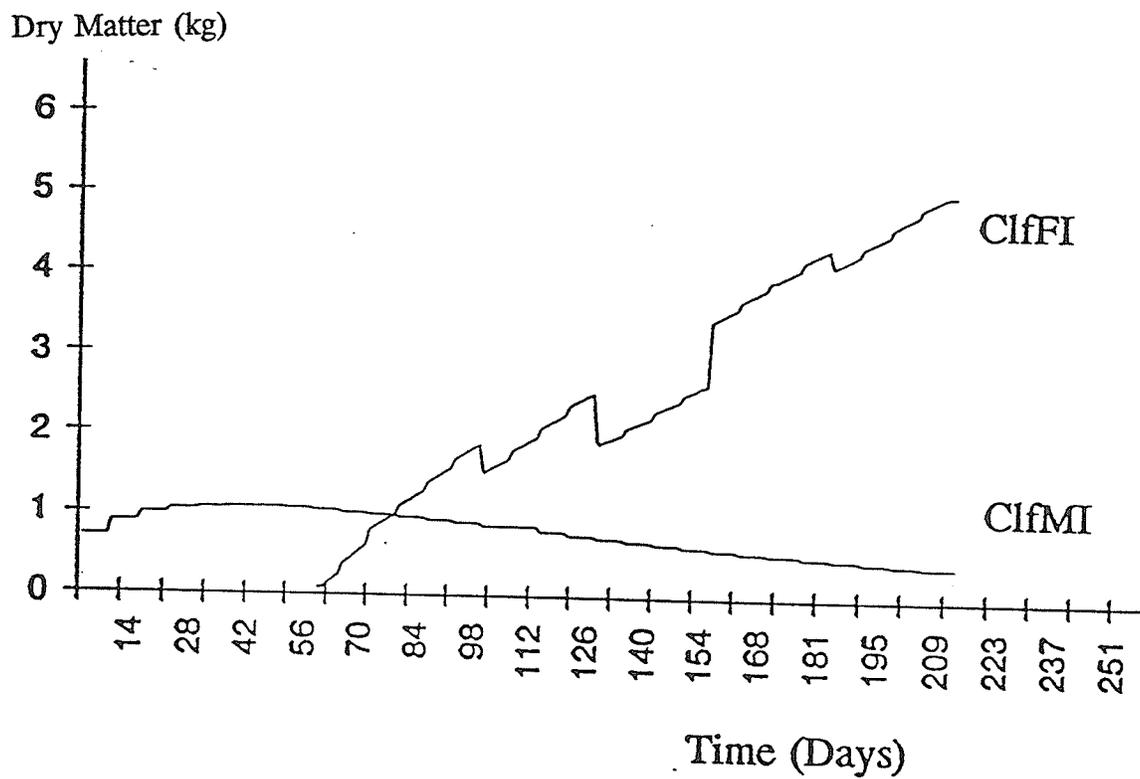


Figure 12. Plot of calf forage dry matter consumption (CifFI) and calf milk dry matter consumption (CifMI).

amounted to only 0.86% increase to the original mean used in the model which is 470 kg (Table 5). This small increase reflects the scaled increase in cow weight as a result of a unit increase in weaning weight defined in the model.

Total milk yield (TMilk) decreased by 3.03 kg and amounted to only 0.23% decrease to the original mean of 1356.80 kg (Table 5). This decrease is a direct consequence of selection based on weaning weight under negative $r_{G:wwd,wwm}$. Barlow (1978), Trus and Wilton (1988) and Johnson et al. (1992) have also commented on this consequence of selection based on weaning weight.

Cow forage dry matter intake (CowFI) increased by 14.11 kg and amounted to 0.50% increase to the original mean used in the model which is 2820 kg (Table 5). This small increase can be attributed to the marginal increase in CowWt (0.86%) and the insignificant decrease (0.45%) in TMilk. The marginal increase in CowFI is therefore mainly due to the small increase in CowWt.

Biological and Economic Efficiency

Biological efficiency was measured as the total amount of dry matter needed to produce a kg of weaning weight. 13.86 kg of forage dry matter was needed to produce a kg of weaned calf. The economic efficiency of animal breeding programmes have been judged in many different ways. It is generally agreed that the costs of providing feed to the cow-calf pair is the most important economic variable for the cow-calf operation (Klosterman 1972). Thus the bioeconomic analysis in this study was entirely based on costs of purchasing forage to meet feed requirements and the benefits or returns obtained

through the sale of weaned calves for each year cycle. Profit can be viewed in simple terms, as gross income from sale of the final product minus costs incurred in producing the product. Net profit calculated using this definition amounted to \$248.21 per cow per year. A simple way of measuring economic efficiency is to calculate the cost to produce 100 kg of the product. It cost \$93.27 to produce 100 kg of weaned calf.

Partial Efficiency

Examining the change in one component independent of the influence of the other component, can provide valuable information on the contribution of the individual components to production efficiency. In addition, with recent developments in mixed model methodology, it is possible to select on direct or maternal components of weaning weight separately. Knowledge of the efficiency of the bioeconomic input-output system to a unit change of the direct or maternal components of weaning weight would be useful in designing selection programmes for efficient beef calf production.

Partial efficiency of the direct component of weaning weight (Table 6). The phenotypic response here was entirely due to the unit increase in the direct component of weaning weight. As only the direct component of weaning weight increased by a unit, there was no change in cow milk yield. Cow weight (CowWt) increased by 1.50 kg which translates to an increase of 0.32 %. Calf weight (WW) increase by 1 kg and amounted to 0.43% increase to the original mean (230 kg) used in the model. The increase in calf weight was directly due to the unit increase in the direct component of

Table 6. Partial efficiency of the direct component of weaning weight

| Variable Name | Variable Definition | Mean or Base Value | Response |
|---------------|------------------------------------|--------------------|----------|
| WW | Calf weaning weight (kg) | 230 | 1 |
| CowWt | Cow weight (kg) | 470 | 1.50 |
| TMilk | Total milk yield (kg) | 1356.80 | 0 |
| CIfMI | Calf milk dry matter intake (kg) | 167.81 | 0 |
| CIfFI | Calf forage dry matter intake (kg) | 402.89 | 2.74 |
| CowFI | Cow forage dry matter intake (kg) | 2811.77 | 5.61 |
| Profit | Profit in dollars (\$ cow-calf) | 244.53 | 1.44 |

weaning weight. **CifMI** decreased by a negligible amount. However, **CifFI** increased by 2.74 kg (0.68%). **CowFI** increased by 5.6 kg (0.2%). In terms of biological efficiency, 13.95 kg of dry matter were needed to produce 1 kg of weaned calf. Net profit increased by \$1.44 (0.59%). In terms of economic efficiency, \$93.52 was required to produce 100 kg of beef calf (Table 6).

Partial efficiency of the maternal component of weaning weight (Table 7). The phenotypic response here was entirely due to the unit increase in the maternal component of weaning weight. A unit increase in the maternal component of weaning weight increased **TMilk** by 29.68 kg (2.19%). As there was no selection pressure on the direct component, there was no change in **CowWt**. **WW** increased by 1 kg (0.43%) and this increase was entirely due to selection pressure on the maternal component of weaning weight. **CifMI** increased by 3.67 kg (2.19%). In contrast, **CifFI** decreased by 3.37 kg (0.84%). **CowFI** increased by 8.72 kg (0.31%). This increase is due to the increase in milk production by the dam. In terms of biological efficiency, 13.94 kg of dry matter was needed to produce 1 kg of weaned calf. Net Profit increased by \$1.65 (0.67%). In terms of economic efficiency, \$93.43 was required to produce 100 kg of beef calf (Table 7).

Partial efficiency of direct and maternal component of weaning weight (Table 8). The phenotypic response here was due to unit increase in both the direct and maternal components of weaning weight. **TMilk** increased by 29.68 kg (2.19%). This increase

Table 7. Partial efficiency of the maternal component of weaning weight

| Variable Name | Variable Definition | Mean or Base Value | Response |
|---------------|------------------------------------|--------------------|----------|
| WW | Calf weaning weight (kg) | 230 | 1 |
| CowWt | Cow weight (kg) | 470 | 0 |
| TMilk | Total milk yield (kg) | 1356.80 | 29.68 |
| ClfMI | Calf milk dry matter intake (kg) | 167.81 | 3.67 |
| ClfFI | Calf forage dry matter intake (kg) | 402.89 | -3.37 |
| CowFI | Cow forage dry matter intake (kg) | 2811.77 | 8.72 |
| Profit | Profit in dollars (\$ cow-calf) | 244.53 | 1.65 |

Table 8. Partial efficiency of the direct and maternal components of weaning weight

| Variable Name | Variable Definition | Mean or Base Value | Response |
|---------------|------------------------------------|--------------------|----------|
| WW | Calf weaning weight (kg) | 230 | 2 |
| CowWt | Cow weight (kg) | 470 | 1.50 |
| TMilk | Total milk yield (kg) | 1356.80 | 29.68 |
| ClfMI | Calf milk dry matter intake (kg) | 167.81 | 3.67 |
| ClfFI | Calf forage dry matter intake (kg) | 402.89 | -0.65 |
| CowFI | Cow forage dry matter intake (kg) | 2811.77 | 14.33 |
| Profit | Profit in dollars (\$ cow-calf) | 244.53 | 3.09 |

is entirely due to the unit increase in the maternal component of weaning weight. CowWt increased by 1.50 kg (0.32%) and was entirely due to the unit increase in the direct component of weaning weight. WW increased by 2 kg, indicating a unit increase in the direct component and a unit increase in the maternal component. Increase in WW amounted to 0.87% of the original mean used in the model. CifMI increased by 3.67 kg (2.19%), while CifFI decreased by 0.65 kg (0.16%). CowFI increased by 14.33 kg (0.51%). In terms of biological efficiency, 13.92 kg of dry matter was needed to produce 1 kg of weaned calf. Net profit increased by \$1.26 (3.08%). In terms of economic efficiency, \$93.26 was needed to produce 100 kg of weaned calf (Table 8).

CifMI decreased by a negligible amount for partial efficiency of the direct component, while for partial efficiency of the maternal component, CifMI increased by 2.19%. In contrast, for partial efficiency of the direct component, CifFI increased by 0.68% while for partial efficiency of the maternal component, CifFI decreased by 0.84%. This contrasting outcome explains the association between CifMI and CifFI in relation to selection pressure applied to either (direct or maternal) components of weaning weight. It seems selection on the maternal component is superior in terms of bioeconomic efficiency than selection only on the direct component. This is probably due to the absence of a correlated increase in cow weight when selection is solely on the maternal component.

Sensitivity of the Bioeconomic Considerations to $r_{G:WWD, WWM}$

Barlow (1978) has commented on the serious lack of knowledge regarding sensitivity of

correlated responses in bioeconomic characteristics to selection for weaning weight, and the clear need for sensitivity analysis with this regard. Sensitivity of the bioeconomic input-output system to incomplete knowledge of $r_{G:WWD,WWM}$ and other assumed parameters were therefore done.

Sensitivity of calf characteristics. Calf weaning weight (WW) was fairly sensitive to lack of knowledge of $r_{G:WWD,WWM}$. WW increased by 2.27% from the original mean for $r_{G:WWD,WWM}=0.4$ and $h^2_D=0.4$ and $h^2_M=0.2$ (Table 9, Table 10). Increase in WW was lowest at $r_{G:WWD,WWM}=-0.4$ and $h^2_D=0.2$ and $h^2_M=0.2$.

CfMI, in general was more sensitive than CfFI. Correlated change in CfMI was highest (3.89%) for $r_{G:WWD,WWM}=0.4$, and $h^2_D=0.2$ and $h^2_M=0.4$ (Table 9, Table 10). In contrast, correlated change in CfFI was highest (1.92%) for $r_{G:WWD,WWM}=-0.4$, and $h^2_D=0.4$ and $h^2_M=0.2$. When $r_{G:WWD,WWM}$ was negative, CfMI and CfFI were inversely related.

Sensitivity of cow characteristics. In general, correlated changes in CowWt were least sensitive to lack of knowledge on $r_{G:WWD,WWM}$. A maximum increase of 1.14% to the original mean was recorded for $r_{G:WWD,WWM}=0.4$, and $h^2_D=0.4$ and $h^2_M=0.2$ (Table 9, Table 10). Lowest correlated change (0.36%) was recorded for $r_{G:WWD,WWM}=-0.4$, and $h^2_D=0.2$ and $h^2_M=0.2$. These results corroborate other findings reported in the literature on the relative insensitivity of CowWt to bioeconomic efficiency (Marshall et al. 1976; Anderson et al. 1983; Dickerson 1978; Dinkel 1988; Lamb et al. 1992). In contrast,

Table 9. Changes in cow and calf characteristics

| h^2_D | h^2_M | $r_{G:WWD,WWM}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
|---------|---------|-----------------|-------|------|-------|-------|-------|-------|--------|
| 0.2 | 0.2 | -0.4 | 1.87 | 1.40 | 4.62 | 0.57 | 2.88 | 8.35 | 2.05 |
| | | 0 | 2.34 | 2.34 | 23.10 | 2.86 | 1.63 | 15.52 | 3.52 |
| | | 0.4 | 2.80 | 3.27 | 41.58 | 5.14 | 0.46 | 22.70 | 4.99 |
| 0.4 | 0.2 | -0.4 | 4.01 | 2.57 | -3.03 | -0.38 | 7.67 | 14.11 | 3.68 |
| | | 0 | 4.67 | 3.89 | 23.10 | 2.86 | 5.88 | 24.24 | 5.77 |
| | | 0.4 | 5.33 | 5.21 | 49.23 | 6.09 | 4.18 | 34.38 | 7.84 |
| 0.2 | 0.4 | -0.4 | 1.68 | 1.79 | 20.07 | 2.48 | 0.77 | 12.16 | 2.72 |
| | | 0 | 2.34 | 3.12 | 46.20 | 5.71 | -0.88 | 22.31 | 4.79 |
| | | 0.4 | 3.00 | 4.44 | 72.35 | 8.95 | -2.40 | 32.45 | 6.86 |

h^2_D Heritability of direct component.

h^2_M Heritability of maternal component.

$r_{G:WWD,WWM}$ Genetic correlation between direct and maternal components of weaning weight.

CowWt Cow weight in kg.

WW Calf weight in kg.

TMilk Total milk yield in kg.

ClfMI Calf milk dry matter intake in kg.

ClfFI Calf dry matter intake in kg.

CowFI Cow forage dry matter intake in kg.

Profit Profit per cow calf.

Table 10. Percent change in cow and calf characteristics

| h^2_D | h^2_M | $r_{G:WWD,WWM}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
|---------|---------|-----------------|-------|------|-------|-------|-------|-------|--------|
| 0.2 | 0.2 | -0.4 | 0.40 | 0.61 | 0.34 | 0.25 | 0.72 | 0.30 | 0.84 |
| | | 0 | 0.50 | 1.02 | 1.70 | 1.24 | 0.41 | 0.55 | 1.44 |
| | | 0.4 | 0.60 | 1.42 | 3.07 | 2.24 | 0.12 | 0.81 | 2.04 |
| 0.4 | 0.2 | -0.4 | 0.86 | 1.12 | -0.23 | -0.17 | 1.92 | 0.50 | 1.51 |
| | | 0 | 1.00 | 1.69 | 1.70 | 1.24 | 1.46 | 0.86 | 2.36 |
| | | 0.4 | 1.14 | 2.27 | 3.63 | 2.65 | 1.04 | 1.23 | 3.21 |
| 0.2 | 0.4 | -0.4 | 0.36 | 0.78 | 1.48 | 1.08 | 0.19 | 0.43 | 1.11 |
| | | 0 | 0.50 | 1.36 | 3.41 | 2.49 | -0.22 | 0.80 | 1.96 |
| | | 0.4 | 0.64 | 1.93 | 5.33 | 3.89 | -0.60 | 1.16 | 2.81 |

h^2_D Heritability of direct component.

h^2_M Heritability of maternal component.

$r_{G:WWD,WWM}$ Genetic correlation between direct and maternal components of weaning weight.

CowWt Cow weight in kg.

WW Calf weight in kg.

TMilk Total milk yield in kg.

ClfMI Calf milk dry matter intake in kg.

ClfFI Calf dry matter intake in kg.

CowFI Cow forage dry matter intake in kg.

Profit Profit per cow-calf.

relative to the other cow characteristics, T_{Milk} was most sensitive to the lack of knowledge on $r_{G:WWD, WWM}$.

Sensitivity Analysis of Bioeconomic Considerations to the Relationship Between Calf and Cow Characteristics

Two main biological parameters in this analysis are the correlation between calf weaning weight and cow weight, and calf weaning weight and cow milk yield. Estimates of these parameters in the literature are scanty for beef cattle. There was therefore a clear need to examine the sensitivity of the model to these parameters.

The direct component of weaning weight reflects the response to selection for growth potential. An increase in this component of weaning weight is expected to increase cow mature weight. This association was expressed as the regression of $CowWt$ on the direct component of WW ($b_{CowWt, WWD}$). In this study it was assumed that 1 kg increase in weaning weight increased cow weight by 1.5 kg. A lower limit (0.17 kg) and an upper limit (3.0 kg) were used to study the sensitivity of the bioeconomic input-output system to the association between calf weight and cow weight.

Changes in the maternal component of weaning weight reflects the response to selection for maternal ability or milk yield in beef cows. This response or genetic change would actually increase the mean milk yield of beef cows. This association was expressed as the regression of $DMilk$ on the maternal component of WW ($b_{DMilk, WWM}$). In this study, it was assumed that for each kg increase in weaning weight due to maternal component a corresponding increase of 0.14 kg of milk yield was added to the mean milk

yield. A lower limit of 0.042 and an upper limit of 0.24 were established to study the sensitivity of the bioeconomic input-output system to the association between calf weight and cow milk yield.

Sensitivity to a Unit Change in the Direct Component

Sensitivity to biological and economic characteristics (Table 11). There was no change in **TMilk**, as the partial increase here was only for the direct component. Increase in **CowWt** was highest when $b_{\text{CowWt, WWD}}=3$ (473.0). Highest **CowFI** was recorded when $b_{\text{CowWt, WWD}}=3$ (2823 kg). Highest **Profit** was recorded when $b_{\text{CowWt, WWD}}=0.17$ (\$246.31) and lowest profit was recorded for $b_{\text{CowWt, WWD}}=3.00$ (\$245.60) (Table 11). The percentage change in all correlated traits were not very different as a result of differences in the regression coefficients indicating that conclusions would not change much due to quite different assumed values for $b_{\text{CowWt, WWD}}$.

Sensitivity to a Unit Change in the Maternal Component

Sensitivity to biological and economic characteristics (Table 12). There was no change in **CowWt**, as the partial increase here was only for the maternal component. **CifMI** was highest for $b_{\text{CowWt, WWD}}=0.24$ (174.10 kg) while **CifFI** was highest for $b_{\text{DMILK, WWM}}=0.04$ (403.97). **CowFI** was highest for $b_{\text{CowWt, WWD}}=0.24$ (2826.71). This may be interpreted as increases in **CowFI** for the increase demand of milk production.

Table 11. Sensitivity of cow and calf characteristics to a unit change in the direct component

| Cow and calf characteristics | | | | | | | |
|------------------------------|--------|--------|---------|--------|--------|---------|--------|
| $b_{\text{CowWt, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.17 | 470.17 | 231.00 | 1356.80 | 167.81 | 405.73 | 2812.40 | 246.31 |
| 1.50 | 471.50 | 231.00 | 1356.80 | 167.81 | 405.73 | 2817.38 | 245.97 |
| 3.00 | 473.00 | 231.00 | 1356.80 | 167.81 | 405.73 | 2823.00 | 245.60 |

| Change in cow and calf characteristics | | | | | | | |
|--|-------|----|-------|-----------|---------|---------|---------|
| $b_{\text{CowWt, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.17 | 0.17 | 1 | 0 | -.0045961 | 2.74217 | 0.6324 | 1.77775 |
| 1.50 | 1.50 | 1 | 0 | -.0045961 | 2.74217 | 5.6133 | 1.44391 |
| 3.00 | 3.00 | 1 | 0 | -.0045961 | 2.74217 | 11.2267 | 1.06768 |

| Percentage change in cow and calf characteristics | | | | | | | |
|---|-------|------|-------|-------|-------|-------|--------|
| $b_{\text{CowWt, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.17 | 0.04 | 0.43 | 0.00 | -0.00 | 0.68 | 0.02 | 0.73 |
| 1.50 | 0.32 | 0.43 | 0.00 | -0.00 | 0.68 | 0.20 | 0.59 |
| 3.00 | 0.64 | 0.43 | 0.00 | -0.00 | 0.68 | 0.40 | 0.44 |

$b_{\text{CowWt, WW D}}$ Regression of CowWt on the direct component of WW.

Table 12. Sensitivity of cow and calf characteristics to a unit change in the maternal component

| Cow and calf characteristics | | | | | | | |
|--|--------|--------|---------|---------|----------|---------|---------|
| $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.04 | 470.00 | 231.00 | 1365.28 | 168.85 | 403.97 | 2814.26 | 246.30 |
| 0.14 | 470.00 | 231.00 | 1386.48 | 171.48 | 399.62 | 2820.49 | 246.18 |
| 0.24 | 470.00 | 231.00 | 1407.68 | 174.10 | 395.35 | 2826.71 | 246.04 |
| Change in cow and calf characteristics | | | | | | | |
| $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.04 | 0 | 1 | 8.48 | 1.04419 | 0.97755 | 2.4870 | 1.77172 |
| 0.14 | 0 | 1 | 29.68 | 3.66615 | -3.36736 | 8.7157 | 1.64546 |
| 0.24 | 0 | 1 | 50.88 | 6.28811 | -7.63761 | 14.9444 | 1.51419 |
| Percent change in cow and calf characteristics | | | | | | | |
| $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | ClfMI | ClfFI | CowFI | Profit |
| 0.04 | 0 | 0.43 | 0.63 | 0.45 | 0.24 | 0.09 | 0.72 |
| 0.14 | 0 | 0.43 | 2.19 | 1.59 | -0.84 | 0.31 | 0.67 |
| 0.24 | 0 | 0.43 | 3.75 | 2.73 | -1.90 | 0.53 | 0.62 |

$b_{\text{DMilk, WW}}$ Regression of DMilk on the maternal component of weaning weight.

Highest profit was recorded for $b_{\text{DMilk,WWM}}=0.04$ (\$246.30) and lowest profit for $b_{\text{DMilk,WWM}}=0.24$ (\$246.04) (Table 12).

Sensitivity to a Unit Change in Direct and Maternal Components

Sensitivity to biological and economic characteristics (Table 13). TMilk was highest for $b_{\text{CowWt,WWD}}=0.24$ (1407.68). CowWt was highest for $b_{\text{CowWt,WWD}}=3.0$ (473 kg). ClfMI was highest for $b_{\text{CowWt,WWD}}=0.24$ (174.10 kg), while ClfFI was highest for $b_{\text{DMilk,WWM}}=0.04$ (406.71 kg). CowFI was highest for $b_{\text{CowWt,WWD}}=3.0$ and $b_{\text{DMilk,WWM}}=0.24$. Highest profit was recorded for the lowest correlations ($b_{\text{CowWt,WWD}}=0.17$ and $b_{\text{DMilk,WWM}}=0.04$). Gradual decrease in profit was observed as the correlation between calf and cow characteristics (Table 13) increased.

The sensitivity analysis provided valuable information on the sensitivity of the biological input-output system to variations in the biological parameters. The assumed values seem reasonable, and were used in simulating bioeconomic response for a structured beef cattle population, as a second part of this research.

Gene-Flow Model

Response to selection. Response to selection was predicted using the gene flow matrix for the hypothetical beef cattle population in Manitoba and the genetic parameters adapted from the work of Trus and Wilton (1988). The gene flow model allowed the

Table 13. Sensitivity of cow and calf characteristics to a unit change in the D, and a unit change in the M component

| Cow and calf characteristics | | | | | | | | |
|---|------------------------|--------|--------|---------|---------|----------|---------|---------|
| $b_{\text{CowWt, WW}}$ | $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | CifMI | CifFI | CowFI | Profit |
| 0.17 | 0.04 | 470.17 | 232.00 | 1365.28 | 168.85 | 406.71 | 2814.89 | 248.08 |
| 0.17 | 0.14 | 470.17 | 232.00 | 1386.48 | 171.48 | 402.34 | 2821.12 | 247.95 |
| 0.17 | 0.24 | 470.17 | 232.00 | 1407.68 | 174.10 | 398.06 | 2827.35 | 247.82 |
| 1.50 | 0.04 | 471.50 | 232.00 | 1365.28 | 168.85 | 406.71 | 2819.87 | 247.74 |
| 1.50 | 0.14 | 471.50 | 232.00 | 1386.48 | 171.48 | 402.34 | 2826.10 | 247.62 |
| 1.50 | 0.24 | 471.50 | 232.00 | 1407.68 | 174.10 | 398.06 | 2832.33 | 247.49 |
| 3.00 | 0.04 | 473.00 | 232.00 | 1365.28 | 168.85 | 406.71 | 2825.33 | 247.37 |
| 3.00 | 0.14 | 473.00 | 232.00 | 1386.48 | 171.48 | 402.34 | 2831.72 | 247.24 |
| 3.00 | 0.24 | 473.00 | 232.00 | 1407.68 | 174.10 | 398.06 | 2837.95 | 247.11 |
| Change in cow and calf characteristics | | | | | | | | |
| $b_{\text{CowWt, WW}}$ | $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | CifMI | CifFI | CowFI | Profit |
| 0.17 | 0.04 | 0.17 | 2 | 8.48 | 1.04419 | 3.71778 | 3.1239 | 3.54537 |
| 0.17 | 0.14 | 0.17 | 2 | 29.68 | 3.66615 | -0.64565 | 9.3526 | 3.42035 |
| 0.17 | 0.24 | 0.17 | 2 | 50.88 | 6.28811 | -4.92814 | 15.5813 | 3.28991 |
| 1.50 | 0.04 | 1.50 | 2 | 8.48 | 1.04419 | 3.71778 | 8.1048 | 3.21153 |
| 1.50 | 0.14 | 1.50 | 2 | 29.68 | 3.66615 | -0.64565 | 14.3335 | 3.08651 |
| 1.50 | 0.24 | 1.50 | 2 | 50.88 | 6.28811 | -4.92814 | 20.5623 | 2.95606 |
| 3.00 | 0.04 | 3.00 | 2 | 8.48 | 1.04419 | 3.71778 | 13.7182 | 2.83530 |
| 3.00 | 0.14 | 3.00 | 2 | 29.68 | 3.66615 | -0.64565 | 19.9469 | 2.71028 |
| 3.00 | 0.24 | 3.00 | 2 | 50.88 | 6.28811 | -4.92814 | 26.1756 | 2.57983 |
| Percentage change in cow and calf characteristics | | | | | | | | |
| $b_{\text{CowWt, WW}}$ | $b_{\text{DMilk, WW}}$ | CowWt | WW | TMilk | CifMI | CifFI | CowFI | Profit |
| 0.17 | 0.04 | 0.87 | 0.04 | 0.63 | 0.45 | 0.92 | 0.11 | 1.45 |
| 0.17 | 0.14 | 0.87 | 0.04 | 2.19 | 1.59 | -0.16 | 0.33 | 1.40 |
| 0.17 | 0.24 | 0.87 | 0.04 | 3.75 | 2.73 | -1.22 | 0.55 | 1.35 |
| 1.50 | 0.04 | 0.87 | 0.04 | 0.63 | 0.45 | 0.92 | 0.29 | 1.31 |
| 1.50 | 0.14 | 0.87 | 0.04 | 2.19 | 1.59 | -0.16 | 0.51 | 1.26 |
| 1.50 | 0.24 | 0.87 | 0.04 | 3.75 | 2.73 | -1.22 | 0.73 | 1.21 |
| 3.00 | 0.04 | 0.87 | 0.04 | 0.63 | 0.45 | 0.92 | 0.49 | 1.16 |
| 3.00 | 0.14 | 0.87 | 0.04 | 2.19 | 1.59 | -0.16 | 0.71 | 1.11 |
| 3.00 | 0.24 | 0.87 | 0.04 | 3.75 | 2.73 | -1.22 | 0.93 | 1.06 |

computation of the mean direct and maternal breeding values of each age and sex group. From these breeding values phenotypic changes in weaning weight of commercial calves were determined. Response was simulated for a period of 20 years based on a single cycle of selection at the beginning of the programme at year zero.

Changes in the phenotypic value of the hypothetical population as well as changes in the magnitude of the direct and the maternal components of weaning weight were computed. Phenotypic response was computed as the sum of the direct and maternal responses which were expressed as kg of change per time unit (year). These responses were simulated for a period of 20 years for a single cycle of selection in year zero (at the start of the programme). The single cycle of selection was intended to represent a simple method of evaluating the changes brought about by selection (Smith 1978; Mitchell et al. 1982). It is an effective way of illustrating genetic change in a hierarchical population (Hill 1974; Mueller and James 1985).

Though the response predicted by the single cycle of selection was small, it clearly demonstrated the nature of response to selection when generations overlap and populations are structured (Figure 13). The pattern of response resembled that predicted by Hill (1976) for a hypothetical beef cattle population. Responses predicted in this study were also erratic in the early years and eventually stabilized with the passage of time. This clearly demonstrates that genetic improvement through selection at the beginning of the programme is not immediately passed to the subsequent generations due to age differences in the selected group. Figure 13 indicates that the response stabilizes or reaches an asymptote around year 14 of the programme. This asymptotic response

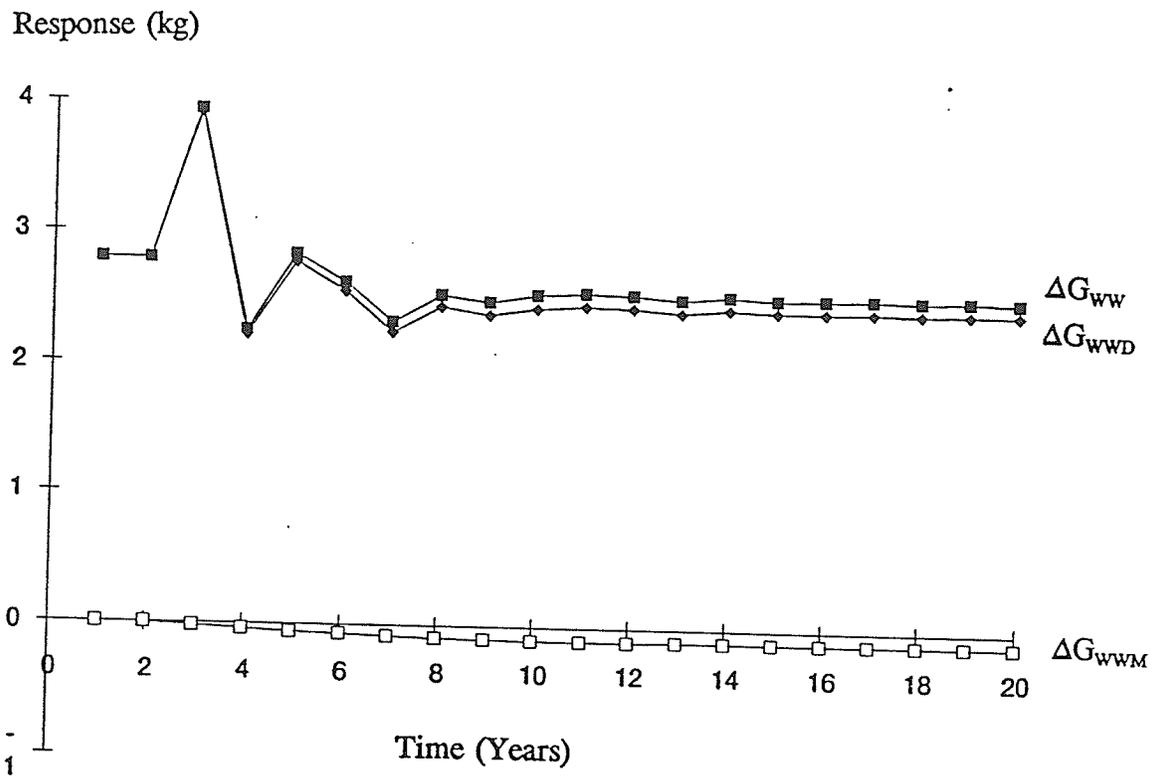


Figure 13. Response in weaning weight (WW) from a single cycle of selection.

is theoretically equivalent to the uniform rate of response predicted by the classical theory (Hill 1974), and is actually not reached till about the end of the programme (Figure 13). The erratic nature of response to selection has important implications in evaluating economic benefits of selection programmes (Figure 13). If response has been predicted using the uniform rate of response methodology (Rendel and Robertson 1950), then predicted response would be the same for each year. Discounted monetary returns would not represent actual returns for each year.

Changes in Biological and Economic Characteristics

Correlated changes to other biological characteristics of the population as a result of response to selection were computed for each year cycle of the 20 year evaluation period. With a single cycle of selection, as expected, the magnitude of change over time was very small.

For the purpose of illustrating the differences between selection and no selection, only characteristics for the last year of the evaluation period (year 20) is discussed. This was done to show the differences since by year 20 the selection response had plateaued.

Changes in calf characteristics. Calf weaning weight (WW) increased by 7.33 kg and amounted to only a 1.07% increase to the original mean used in the model which is 230 kg (Table 14). Clffi increased by 7.33 kg and amounted to a 1.82% increase to the original mean used in the model which is 402.99 kg (Table 14).

Table 14. Changes in cow and calf characteristics for the last year (Year 20) of the evaluation period

| | CowWt | WW | TMilk | CIfMI | CIfFI | CowFI |
|----------|--------|--------|---------|---------|--------|---------|
| Year 20 | 473.82 | 232.45 | 1353.91 | 167.45 | 410.32 | 2825.22 |
| Base | 470.00 | 230.00 | 1356.80 | 167.81 | 402.99 | 2811.77 |
| Change | 3.82 | 2.45 | -2.89 | -0.36 | 7.33 | 13.45 |
| % Change | 0.813% | 1.07% | -0.213% | -0.215% | 1.82% | 0.48% |

Changes in cow characteristics. Cow weight increased by 3.82 kg and amounted to only a 0.83% increase to the original mean used in the model which is 470 kg (Table 14). **TMilk** yield decreased by 2.89 kg and amounted to a 0.21% decrease to the original mean which is 1356.80 (Table 14). **CowFI** increased by 13.45 kg and amounted to a 0.48% increase to the original mean used in the model which is 2811.77 kg (Table 14).

A major consequence of selection for weaning weight, when $r_{G:WWD, WWM}$ is negative is the reduction in milk yield. As a result **CifMI** is reduced and **CifFI** is increased.

Selection programmes usually span long periods of time. The applicability and rationality of using the discounting technique in evaluating the benefits of selection may be illustrated with the help of the results presented in Table 15, Figure 14. Net monetary benefits in the early years are discounted least and thus relatively larger benefits are obtained in the early years. Therefore, the returns from the latter years are relatively smaller. However, they do contribute substantially to the overall total benefits that may be obtained just from a single cycle of selection. The total monetary value is a better indicator of the benefits of selection in the long run (Hill 1974). The accumulated net discounted returns clearly show the benefits of selection for weaning weight.

Table 15. Discounted returns per calf from a single cycle of selection

| Year | Discount Rate | No Selection | | Selection | |
|------|---------------|--------------|-------------------|-----------|-------------------|
| | | Profit | Cumulative Profit | Profit | Cumulative Profit |
| 1 | 0.96154 | 235.13 | 235.13 | 239 | 239 |
| 2 | 0.92456 | 226.08 | 461.21 | 229.81 | 468.81 |
| 3 | 0.889 | 217.39 | 678.60 | 222.4 | 691.21 |
| 4 | 0.8548 | 209.02 | 887.62 | 211.76 | 902.97 |
| 5 | 0.82193 | 200.99 | 1,088.61 | 204.27 | 1,107.24 |
| 6 | 0.79031 | 193.25 | 1,281.86 | 196.16 | 1,303.40 |
| 7 | 0.75992 | 185.82 | 1,467.68 | 188.28 | 1,491.68 |
| 8 | 0.73069 | 178.68 | 1,646.36 | 181.24 | 1,672.92 |
| 9 | 0.70259 | 171.8 | 1,818.16 | 174.22 | 1,847.14 |
| 10 | 0.67556 | 165.19 | 1,983.35 | 167.56 | 2,014.70 |
| 11 | 0.64958 | 158.84 | 2,142.19 | 161.14 | 2,175.84 |
| 12 | 0.6246 | 152.73 | 2,294.92 | 154.93 | 2,330.77 |
| 13 | 0.60057 | 146.86 | 2,441.78 | 148.95 | 2,479.72 |
| 14 | 0.57748 | 141.21 | 2,582.99 | 143.25 | 2,622.97 |
| 15 | 0.55526 | 135.78 | 2,718.77 | 137.72 | 2,760.69 |
| 16 | 0.53391 | 130.56 | 2,849.33 | 132.43 | 2,893.12 |
| 17 | 0.51337 | 125.53 | 2,974.86 | 127.34 | 3,020.46 |
| 18 | 0.49363 | 120.71 | 3,095.57 | 122.44 | 3,142.90 |
| 19 | 0.47464 | 116.06 | 3,211.63 | 117.73 | 3,260.63 |
| 20 | 0.45639 | 111.6 | 3,323.23 | 113.2 | 3,373.83 |

Net Returns (Dollars)

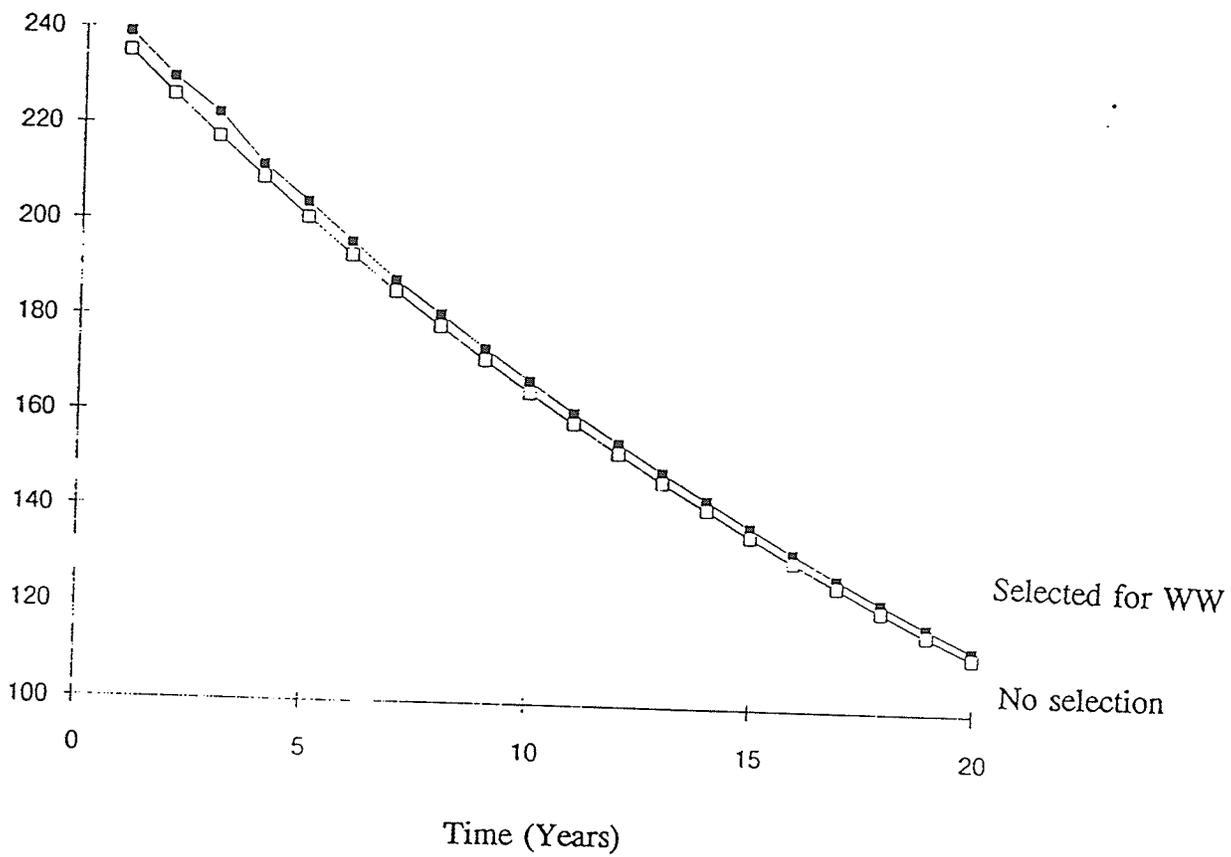


Figure 14. Discounted returns from a single cycle of selection.

SUMMARY AND CONCLUSIONS

The purpose of this study was to evaluate the consequences of selection for weaning weight on the bioeconomic efficiency of beef calf production using a deterministic simulation model. Weaning weight is composed of direct and maternal components. Methods were developed to estimate relative genetic gain of the direct and maternal components of weaning weight after a single cycle of selection on weaning weight. Genetic parameters relevant to the Canadian environment were assumed in simulating response to selection.

Though reports in the literature tend to support a negative genetic correlation, a wide range of correlations have been reported. A range of heritability estimates for the direct and maternal components have also been reported. A sensitivity analysis was therefore performed using a range of heritability and correlation estimates. There is a lack of certainty of the magnitude of the heritability estimates and the magnitude and sign of the genetic correlation. This may be due to differences in parameters among populations or to large sampling variances of estimates but whatever the reason it is important to know the consequences that a selection program has for efficiency over the range of possible genetic parameters. This sensitivity analysis provided valuable information on the consequences of selection for weaning in terms of direct, maternal and total phenotypic response. The sensitivity analysis highlights the detrimental effects of a negative genetic correlation between the direct and maternal components. Under these circumstances, selection favouring one component of weaning weight would have an adverse affect on the other component. A positive genetic correlation between D and M

would result in maximum phenotypic, direct and maternal response.

Phenotypic response to selection was positive which was contributed entirely by the gain in the direct component of weaning weight. However, the phenotypic response was lower than the direct response due to genetic loss through the maternal component. The lower phenotypic response was due to the negative genetic correlation between the direct and maternal components of weaning weight. To evaluate the bioeconomic efficiency of the genetic response to selection, correlated changes in the biological characteristics and economic outcomes were computed. Cow and calf feed requirements in terms of forage dry matter intake were calculated for a 365 day cycle. In calculating calf feed requirements, the relationship between calf milk dry matter intake and calf forage dry matter intake were taken into consideration. Biological efficiency was measured as the total amount of dry matter needed to produce a kilogram of calf weaning weight. Economic efficiency was calculated as the cost needed to produce per 100 kg of weaned calf. A net benefit was recorded as a result of selection on weaning weight. Both biological and economic efficiency indicators showed positive increases as a result of selection. However, this was at the expense of an increase in cow weight and a decrease in milk production.

Sensitivity of the bioeconomic input-output system to variations in the direct/maternal correlation was also examined. Positive genetic correlation between the direct and maternal components of weaning weight was most advantageous in terms of improvement of bioeconomic efficiency. However, correlated changes in cow weight was also dramatic as was milk yield.

Partial efficiency was defined as changes in the bioeconomic input-output system to a unit increase of the direct or maternal components of weaning weight. Partial bioeconomic efficiency due to improving the maternal component was marginally superior to the partial bioeconomic efficiency of improving the direct component. This was probably due to the absence of a correlated increase in cow weight when selection pressure is solely on the maternal component.

Sensitivity of the bioeconomic input-output system to the assumed correlations between cow and calf characteristics was examined. The assumed correlations between calf weaning weight and cow weight, and calf weaning weight and cow milk yield were found to be reasonable.

It is demonstrated from this study that when selection is based on weaning weight, under the circumstances of negative genetic correlation between direct and maternal components, there will be a reduction in milk yield, though phenotypic and bioeconomic response would be positive. The consequences of selection based on calves' weaning weights alone, in the long run, is the reduction in total milk yield of beef cows. Consequences for beef breeds, especially those with relatively low milk yields like the Canadian Hereford could be drastic.

In Canada, EPD's (Expected Progeny Difference) for direct and maternal genetic effects are now available through the Record of Performance programme (Agriculture Canada 1993). These values are calculated using all available weaning weight records on relatives of an animal, i.e. weaning weight records of maternal sibs of the calf, the calves of the daughters of the calf's sire, maternal grandsire and paternal grandsire as

well as more distant relatives. The EPD's could be utilized to select calves designed as a special maternal group for special situations where there may be a need to improve milk yield. There are many countries, especially in the developing world, where EPD's are not available, where selection is simply based on weaning weight of the calf. In beef breeds with relatively low milk yields under circumstances of negative genetic correlation between direct and maternal, the consequences in the long term can be far reaching. The findings from this research, especially the sensitivity analysis of the genetic and biological parameters of weaning weight should provide valuable information in designing long term breeding goals for maximising cow-calf productivity.

Beef cattle populations are known to be structured. With overlapping generations, genetic improvement through selection at the beginning of the programme is not immediately passed to subsequent generations at all levels in the population. The genetic and biological parameters which were tested for their sensitivity in the base model were therefore used to construct a Gene-Flow Model. The structure of the Manitoba beef cattle population was obtained from a survey carried out by the Manitoba Department of Agriculture describes strata-nucleus and commercial. This and other relevant information obtained from the literature were used to define the breeding and gene flow activity of a hypothetical beef cattle population. Gene-flow through the population was described with a matrix which accounted for the passage of genes from each source group to its final destination through the different sex and age groups and strata of the population. Response to a single cycle of selection was simulated for an evaluation period of 20 years. Predicted response was erratic in the early years and eventually stabilized with

the passage of time.

The Gene-Flow Model clearly demonstrated that genetic improvement through selection at the beginning of the programme is not immediately passed to subsequent generations due to age difference in the selected group. The response stabilized or reached asymptote around year 15 after a single cycle of selection in year one. This asymptotic response is theoretically equivalent to the uniform rate of response predicted by the Base Model used in the first part of this study. Similar to the Base Model, there was positive response to selection, though there was genetic loss (decrease) in the maternal component due to the negative genetic correlation between the direct and maternal components. That the adoption of the gene flow concept facilitated the application of the discounting technique in beef cattle simulation research is clearly demonstrated in the study. The accumulated net discounted returns indicate that on a cow-calf basis, selection for weaning weight would be more beneficial than no selection, even under negative genetic correlation between direct and maternal components of weaning weight.

LITERATURE CITED

- ANDERSON, V.L., JOST, L., DINKEL, C.A. and BROWN, M.A. 1983. Prediction of daily total digestible nutrient requirement of beef cows in northern climates. *J. Anim. Sci.* 56: 271-279.
- AGRICULTURE CANADA. 1993. Canadian Beef Sire Evaluation Program.
- ARMSTRONG, S.L., WILTON, J.W., SCHAEFFER, L.R. and PFEIFFER, W.C. 1990. Feed intake, weaning weight and net returns comparison for four breeding systems. *J. Anim. Sci.* 68:1848-1856.
- BARLOW, R. 1978. Biological ramification of selection for preweaning growth in cattle. A Review. *Anim. Breeding Abstr.* 469-491.
- BAKER, R.L. 1980. The role of maternal effects on the efficiency of selection in beef cattle. A review. *Pro. New Zealand Soc. Anim. Prod.* 40: 285-303.
- BAKER, R.D., Le DU, Y.L.P., and BARKER, J.M. 1976. Milk fed calves. 1. The effect of milk intake upon the herbage intake and performance of grazing calves. *J. Agric. Sci. (Camb.)* 87: 187-196.
- BARKER, J.S.F., and DAVEY, G.P. 1960. The breed structure and genetic analysis of the pedigree cattle breeds in Australia. II. The Poll Hereford. *Aust. J. Agric. Res.* 11: 1072-1100.
- BEAL, W.E., NOTTER, D.R. and AKERS, R.M. 1990. Techniques for estimation of milk yield in beef cows and relationships of milk yield to calf weight gain and postpartum reproduction. *J. Anim. Sci.* 68:937-943.
- BIRD, J.W.N., and MITCHELL, G. 1980. The choice of discount rate in animal breeding investment appraisal. *Anim. Breed. Abstr.* 48: 499-505.
- BOEHLJE, M.D., and EIDMAN, V.R. 1983. *Farm Management*. John Wiley & Sons. Toronto.
- BOGG, D.L., SMITH, E.F., SCHALLES, R.R., BRENT, B.E., CORAH, L.R., and PRUITT, R.J. 1980. Effects of milk and forage intake on calf performance. *J. Anim. Sci.* 51: 550-553.
- BOURDON, R.M. 1988. Bovine nirvana - From the perspective of a modeler and purebred breeder. *J. Anim. Sci.* 66:1892-1898.

- BRADFORD, C.E. 1972. The role of maternal effects in animal breeding. VII. Maternal effects in sheep. *J. Anim. Sci.* 35: 1324-1334.
- BRASCAMP, E.W. 1975. Model calculations concerning economic optimization of A.I. breeding with cattle. Agric. Res. Rep. 846. Centre Agric. Pub. & Docu. Wageningen. Netherlands.
- BRODY, S. 1942. Bioenergetics and growth. Reinhold Publishing Co. New York.
- BUTSON, S., BERG, R.T., and HARDIN, R.T. 1980. Factors influencing weaning weights of range beef and dairy-beef calves. *Can. J. Anim. Sci.* 60: 727-742.
- CANTET, R.J.C., SCHAEFFER, L.R. and SMITH, C. 1992. Reduced Animal Model with Differential Genetic Grouping for Direct and Maternal Effects. *J. Anim. Sci.* 70:1730-1741.
- CARTWRIGHT, T.C. 1970. Selection criteria for beef cattle in the future. *J. Anim. Sci.* 30: 706-711.
- CARTWRIGHT, T.C. 1978. Systems analysis in animal breeding. *J. Anim. Sci.* 49: 817-825.
- CLUTTER, A.C., and NIELSEN, M.K. 1987. Effects of level of beef cow milk production on pre and postweaning calf growth. 64: 1313-1323.
- CSAKI, C. 1985. Simulation and systems analysis in agriculture. Elsevier. New York.
- CUNNINGHAM, E.P., and RYAN, J. 1975. A note on the effect of the discount rate and length of the accounting period on the economic value of genetic improvement in cattle populations. *Anim. Prod.* 21: 77-80.
- DAVEY, G.P. and BARKER, J.S.F. 1963. The breed structure and genetic analysis of the pedigree cattle breeds in Australia. III. The Hereford. *Aust. J. Agric. Res.* 14: 93-118.
- DESSE, R.E., and KOGER, M. 1967. Maternal effects on preweaning growth rate in cattle. *J. Anim. Sci.* 26:250-253.
- DIAZ, C., NOTTER, D.R. and BEAL, W.E. 1992. Relationship between milk expected progeny difference of Polled Hereford sires and actual milk production of their crossbred daughters. *J. Anim. Sci.* 70:396-402.
- DICKERSON, G.E., and HAZEL, L.N. 1944. Effectiveness of selection on progeny performance as a supplement to earlier culling in livestock. *J. Agric. Res.* 69: 459-476.

- DICKERSON, G.E. 1947. Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. Res. Bull. Iowa. Agric. Exp. Sta. 354: 489-524.
- FOSTER, T.G., MOWAT, D.N., JONES, S.D.M., WILTON, J.W., and STONEHOUSE D.P. 1984. Systems for producing leaner beef. Agric. Sys. 15: 171-181.
- FOX, D.G., SNIFFEN, C.J., and O'CONNOR, J.D. 1988. Adjusting nutrient requirements of beef cattle for animal and environmental variations. J. Anim. Sci. 66: 1475-1495.
- FREKING, B.A. and MARSHALL, D.M. 1992. Interrelationships of heifer milk production and other biological traits with production efficiency to weaning. J. Anim. Sci. 70:646-655.
- GEARHEART, W.W., KELLER, D.S. and SMITH C. 1990. The use of Elite Nucleus Units on Beef Cattle Breeding. J. Anim. Sci. 68:1229-1236.
- GIFFORD, W. 1949. Importance of high milk production in beef cows overestimated. J. Anim. Sci. 8: 605-606.
- GLEDDIE, V.M. and BERG, R.T., 1968. Milk production in range beef cows and its relationships to calf gains. Can. J. Anim. Sci. 48: 323-333.
- GOONEWARDENE, L.A., BERG, R.T., and HARDIN R.T. 1981. A growth study of beef cattle. Can J. Anim. Sci. 61: 1041-1048.
- GRILICHES, Z. 1957. Hybrid Corn: An exploration in the economics of technological change. Econometrica 25: 501-522.
- HARRIS, D.L. 1970. Breeding for efficiency in livestock production: defining the economic objectives. J. Anim. Sci. 30: 860-865.
- HARRIS, D.L., STEWART, T.S., and ARBOLEDA, C.R. 1984. Animal breeding programs. Systematic approach to their design. U.S.D.A. - A.R.S. AAT-NC-8.
- HARRIS, D.L., and STEWART, T.S. 1986. The role of computer simulation and laboratory animals in the design of breeding programs. 3rd. World Cong. on Gen. Appl. to Livest. Prod. XII: 257-268. Lincoln.
- HILL, J.R. 1965. The inheritance of maternal effects in beef cattle. Ph.D. Thesis, North Carolina State University, Raleigh.

- HILL, W.G. 1971. Investment appraisal for national breeding programmes. *Anim. Prod.* 13: 37-50.
- HILL, W.G. 1974. Prediction and evaluation of response to selection with overlapping generations. *Anim. Prod.* 18: 117-139.
- HILL, W.G. 1976. Selection with overlapping generations. *Int. Conf. Quant. Genet. Ames. Iowa.* 367-377.
- HINKS, C.J.M, 1971. The genetic and financial consequences of selection amongst dairy bulls in artificial insemination. *Anim. Prod.* 13:209-218.
- HOHENBOKEN, W.D., and BRINKS, J.S. 1971. Relationships between direct and maternal effects on growth in Herefords. II. Partitioning of variance between relatives. *J. Anim. Sci.* 32: 26-
- HOHENBOKEN, W.D. 1985. Maternal effects. Pages 135 to 149 in *World Animal Science. A. Basic Information. 4. General and Quantitative Genetics.* Ed. A.B. Chapman. Elsevier. New York.
- IRGANG, R., DILLARD, E.V., TESS, M.W., and ROBISON O.W. 1985. Selection for weaning weight and postweaning gain in Hereford cattle. I. Population structure and selection applied. *J. Anim. Sci.* 60: 1133-1141.
- JAMES, R.W. 1972. Optimum selection intensity in breeding programmes. *Anim. Prod.* 14: 1-9.
- JEFFERY, H.B., and BERG, R.T. 1971. Evaluation of milk variables as measure of milk effects on preweaning performance of beef cattle. *Can. J. Anim. Sci.* 51: 21-30.
- JENKINS, T.G. and FERRELL, C.L. 1992. Lactation Characteristics of Nine Breeds of Cattle Fed Various Quantities of Dietary Energy. *J. Anim. Sci.* 70:1652-1660.
- JOHNSON, Z.B., WRIGHT, W.D., BROWN, C.J., BERTRAND, J.K. and BROWN, A.H., JR. 1992. Effect of Including Relationships in the Estimation of Genetic Parameters of Beef Calves. *J. Anim. Sci.* 70:78-88.
- KLOSTERMAN, E.W. 1972. Beef cattle size for maximum efficiency. *J. Anim. Sci.* 34: 875-880.
- KOCH, R.M. 1972. The role of maternal effects in animal breeding: VI. Maternal effects in beef cattle. *J. Anim. Sci.* 35: 1316-1323.
- KOCH, R.M., GIBB, J.B., and GOSEY, J.A. 1986. Evaluation of beef cattle industry

- breeding programs. Breeders and Breed Associations. Third World Congress on Genetics Applied to Livestock Production. IX: 398-409.
- KOCH, R.M., and CLARK R.T. 1955. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. *J. Anim. Sci.* 14: 979-996.
- KOOTS, K.R., and CROW, G.H. 1990. Breed structure of pedigree Hereford cattle in Canada. *Can. J. Anim. Sci.* 69:627-634.
- KROMANN, R.P. 1973. Evaluation of net energy systems. *J. Anim. Sci.* 37: 200-217.
- LAMB, M.A., TESS, M.W. and ROBISON, O.W. 1992. Evaluation of Mating Systems Involving Five Breeds of Integrated Beef Production Systems: Cow-calf Segment. *J. Anim. Sci.* 70:686-699.
- LEGATES, J.E. 1972. The role of maternal effects in animal breeding: IV. Maternal effects in laboratory species. *J. Anim. Sci.* 35: 1294-1302.
- LOFGREEN, G.P., and GARRETT, W.N. 1968. A system of expressing net energy requirements and feed values for growing and finishing beef cattle. *J. Anim. Sci.* 27: 793-806.
- LONG, C.R., and FITZHUGH, H.A. Jr. 1970. Efficiency of alternative beef breeding systems. Beef cattle research in Texas. 1970: 55-60. *Tex. Agr. Exp. Sta. Texas A & M Univ., College Station. Texas.*
- LONG, C.R., CARTWRIGHT, T.C., and FITZHUGH, H.A. Jr. 1975. Systems analysis of sources of genetic and environmental variation in efficiency and beef production: cow size and herd management. *J. Anim. Sci.* 40: 409-420.
- MANGUS, W.L., and BRINKS, J.S. 1971. Relationship between direct and maternal effects on growth in Hereford. 1. Environmental factors during preweaning growth. *J. Anim. Sci.* 32:17-25.
- MANITOBA DEPARTMENT OF AGRICULTURE. 1986
- MARSHALL, D.A., PARKER, W.R., and DINKEL, C.A. 1976. Factors affecting efficiency to weaning in Angus, Charolais and reciprocal cross cows. *J. Anim. Sci.* 43: 1176-1187.
- McMORRIS, M.R., and WILTON, J.W. 1986. Breeding systems, cow weight and milk yield effects on various biological variables in beef production. *J. Anim. Sci.* 63: 1361-1372.

- MELTON, A.A., RIGGS, J.R., NELSON, L.A. and CARTWRIGHT, T.C. 1967. Milk production, composition and calf gains of Angus, Charolais and Hereford cows. *J. Anim. Sci.* 26: 804-809.
- MEYER, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livestock Production Science* 31:179-204.
- MITCHELL, G., SMITH, C., MAKOWER, M., and BIRD, P.J.W.N. 1982. An economic appraisal of pig improvement in Great Britain. *Anim. Prod.* 35: 215-224.
- MONDRAGON, I., WILTON, J.W., ALLEN, O.B., and SONG, H. 1983. Stage of lactation effects, repeatabilities and influences of weaning weights on yield and composition of milk in beef cattle. *Can. J. Anim. Sci.* 63: 751-761.
- MRODE, R.A. 1988. Selection experiments in Beef Cattle. Part 2: A review of responses and correlated responses. *Animal Breeding Abstracts* No. 3, Vol. 56, No. 3, 155-167.
- MUELLER, J.P., and JAMES, J.W. 1985. Phenotypic response to selection for traits with direct and maternal components when generations overlap. *Theoret. Appl. Genet.* 70: 123-127.
- NATIONAL ACADEMY OF SCIENCES - NATIONAL RESEARCH COUNCIL. 1984. Nutrient requirements of beef cattle. (6th. Revised Ed.) National Academy Press. Washington, D.C.
- NOTTER, D.R., CUNDIFF, L.V., SMITH, G.M., LASTER, D.B., and GREGORY, K.E. 1978. Characterization of biological types of cattle. VII. Milk production in young cows and transmitted and maternal effects on preweaning growth of progeny. *J. Anim. Sci.* 46: 908-921.
- NOTTER, D.R., SANDERS, J.O., DICKERSON, G.E., SMITH, G.M., and CARTWRIGHT, T.C. 1979. Simulated efficiency of beef production for a mid-western cow - calf - feedlot management system. I. Milk production. *J. Anim. Sci.* 49: 70-82.
- OLTHOFF, J.C., CROW, G.H., and RAHNEFELD, G.W. 1990. Effect of Including Relationships in the Estimation of Genetic Parameters of Beef Calves. *J. Anim. Sci.* 70:78-88.
- OZKUTUK, K. and BICHARD, M. 1977. Studies of pedigree Hereford cattle breeding. I. Herdbook Analysis. *Anim. Prod.* 24: 1-13.

- PETERSON, P.H., CHRISTENSEN, L.G., ANDERSON, B.B., and OVESEN, E. 1974. Economic optimisation within a dual-purpose cattle population. *Acta. Agric. Scand.* 24: 247-258.
- POUTOUS, M. and VISSAC, B. 1962. A theoretical study of conditions of maximum profitability in progeny testing of artificial insemination in bulls. *Annales de Zootechnic* 11: 233-250.
- RAE, A.L. 1982. Breeding. Pages to in *World Animal Science. Production systems approach. Sheep and goat production.* Editor E.E. Coop. Elsevier. New York. 494 pp.
- RENDEL, J.M. and ROBERTSON, A. 1950. Estimation of genetic gains in milk yield by selection in a closed herd of dairy cattle. *J. Genet.* 50: 1-8.
- REYNOLDS, W.L., DeROUEN, T.M., and BELLOWS, R.A. 1978. Relationships of milk yield of dam to early growth rate of straightbred and crossbred calves. *J. Anim. Sci.* 47: 584-594.
- ROBERTSON, A. 1953. A numerical description of breed structure. *J. Agric. Sci. (Camb.)* 4: 334-336.
- ROBISON, O.W. 1972. The role of maternal effects in animal breeding: V. Maternal effects in swine. *J. Anim. Sci.* 35: 1303-1315.
- ROBISON, O.W. 1981. The influence of maternal effects on the efficiency of selection. A review. *Livest. Prod. Sci.* 8: 121-137.
- ROGERS, L.F. 1972. Economics of replacement rates in commercial beef herds. *J. Anim. Sci.* 34: 921-925.
- RUTLEDGE, J.J., ROBISON, O.W., AHLSCHEDE, W.T., and LEGATES, J.E. 1971. Milk yield and its influence on 205 day weight of beef calves. *J. Anim. Sci.* 33: 563-567.
- SEJRSEN, R. 1978. Mammary development and milk yield in relation to growth rate in dairy and dual purpose heifers. *Acta. Agric. Scand.* 28: 41.
- SIMM, G., YOUNG, M.J., and BEATSON, P.R. 1988. An economic selection index for lean meat production in New Zealand. 45: 465-475.
- SMITH, C. 1978. The effect of inflation and form of investment on the estimated value of genetic improvement in farm livestock. *Anim. Prod.* 26: 101-110.
- SMITH, C., GIBSON, A., and MITCHELL, G. 1982. An economic appraisal of pig

- improvement in Great Britain. 2. Factors affecting estimated benefits. *Anim. Prod.* 35: 225-230.
- SMITH, G.H., and HARRISON, V.L. 1978. The future of livestock systems analysis. *J. Anim. Sci.* 46: 807-811.
- SOLLER, M., BAR-ANAN, R., and PASTERNAK, H. 1966. Selection of dairy cattle for growth rate and milk production. *Anim. Prod.* 8: 109-119.
- SPELLBRING, M.C., MARTIN, T.G., and DREWRY, K.J. 1977. Maternal productivity of crossbred Angus x milking Shorthorn cows. I. Cow and calf weights and scores. *J. Anim. Sci.* 45: 969-975.
- TOLL, G.L., and BARKER, J.S.F. 1979. Genetic history of the pedigree Poll Hereford breed in Australia; Effect of the importation ban. *Aust. J. Agric. Res.* 30: 767-777.
- TRUS, D., and WILTON, J.W. 1988. Direct and maternal effects in beef cattle. *Can J. Anim. Sci.* 68: 119-128.
- VAN VLECK, L.D. 1973. Selection for direct and maternal genetic effects. Pages 133-148 in *Genetics Lectures, Volume 3*. Ed. R. Bogart, Oregon State Univ. Press, Corvallis, Oregon.
- VAN VLECK, L.D., ST. LOUIS, D., and MILLER, J.I. 1977. Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal genetic effects. *J. Anim. Sci.* 44: 360-367.
- VESELY, J.A., and ROBISON, O.W. 1971. Genetic and maternal effects on preweaning growth and type scores in beef calves. *J. Anim. Sci.* 32: 825-831.
- WEINBACH, A.P. 1941. The human growth curve. I. Prenatal growth. *Growth* 5: 217-233.
- WILLHAM, R.L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19: 18-27.
- WILLHAM, R.L. 1972. Beef milk production for maximum efficiency. *J. Anim. Sci.* 34: 864-869.
- WILLHAM, R.L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35: 1288-1293.
- WILLHAM, R.L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7: 405-418.

- WILLHAM, R.L. 1986. Genetic prediction for beef in United States. Third World Congress on Genetics Applied to Livestock Production. IX: 442-445. Lincoln.
- WILTON, J.W. 1979. The use of production systems analysis in developing mating plans and selection goals. *J. Anim. Sci.* 49: 809-816.
- WILTON, J.W., MORRIS, C.A., JENSON, E.A., LEIGH, A.O., and PFEIFFER, W.C. 1974. A linear programming model for beef cattle production. *Can J. Anim. Sci.* 54: 693-707.
- WILTON, J.W., and MORRIS, C.A. 1976. Effects of reproductive performance and mating system on farm gross margins in beef production. *Can. J. Anim. Sci.* 56: 171-186.
- WILTON, J.W., and MONDRAGON, I. 1981. Milk yield and composition of several breeds and crosses of beef cows. Annual Research Report. Univ. of Guelph. Guelph.
- WOOD, P.D.P. 1969. Factors affecting the slope of the lactation curve in cattle. *Anim. Prod.* 11: 307-316.
- WRIGHT, H.B., POLLAK, E.J., and QUAAS, R.L. 1987. Estimation of variance and covariance components to determine heritabilities and repeatabilities of weaning weight in American Simmental cattle. *J. Anim. Sci.* 65: 975-981.