ESTIMATES OF
PHENOTYPIC AND GENETIC PARAMETERS IN
BALI BEEF CATTLE

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ABSTRACT

The study analysed records on weaning (3803) and yearling weight (2990) of beef cattle (*Bibos banteng*) from the Bali Cattle Improvement Project. The main purpose of the study was to derive heritability estimates and phenotypic and genetic correlations between weaning and yearling weights for inclusion in a selection index. Variance components were estimated by Henderson's Method III and REML methods.

Village, year of birth, sex and age (as a covariate) of the calf significantly ($P < .05$) affected weaning weight. Age of dam had a small effect ($P = .08$) while season of birth had no significant effect on weaning weight. Village, year of birth, age of dam, sex and age of the calf as a covariate significantly ($P < .05$) affected yearling weight while season of birth had no significant effect. When first order interactions among fixed effects were included in the model for weaning weight, village by year, village by season, year by season, year by sex of the calf and dam age by season and by sex of the calf were significant ($P < 0.05$). For yearling weight, village by year, season of birth, age of dam and sex of the calf, sex by year of birth and age of dam and season of birth by age of dam interactions were significant ($P < 0.05$).

Least squares means (LSM) ± standard error (SE) for weaning and yearling weight by village contemporary group ranged from 79.4 ± 1.18 kg to 94.4 ± 1.08 kg and from 124.1 ± 1.7 kg to 153.8 ± 1.7 kg, respectively. Weaning and yearling weight LSM ± SE (kg) for years of birth of 1983, 1984, 1985, 1986 and 1987 ranged from 77.6 ± 82 and 134.8 ± .86 to 88.6 ± .51 and 147.1 ± 1.03, respectively. The LSM ± SE (kg) of weaning weight of calves from dam with age 2, 3 and more than 3 years were 83.9 ± 1.16, 85.4 ± .43 and 86.1 ± .30, respectively. LSM ± SE (kg) of yearling weight of those dams were 140.4 ± 1.72, 134.7 ± .68 and 139.4 ± .48,

respectively. The LSM ± SE (kg) of weaning and yearling weight for bull and heifer calves were 89.8 ± .49 and 145.5 ± .75, and 80.5 ± .49 and 130.9 ± .75, respectively.

Age at weighing as a covariate was highly significant (P < 0.01) for both weaning and yearling weights. Regression coefficients of weaning weight and yearling weight on age were .30 kg / day and .20 kg / day, respectively.

Heritability estimates obtained by Henderson's Method III for weaning and yearling weights were .11 ± .03 and .13 ± .04, respectively, and the genetic correlation was estimated as .64 ± .10, respectively. REML estimates were similar. The phenotypic correlation between weaning and yearling weights was .32. There have been no previously reported estimates of these parameters for Bali cattle. However, these parameter estimates fell into the lower end of the ranges reported in the literature for other cattle breeds.

Selection of animals based on a selection index including weaning and yearling weight would lead to increases in both carcass weight and fat depth. Increases in fat depth did not offset the increased payment for carcass weight. The use of a restricted index for keeping fat depth unchanged was also examined, but this severely restricted the gain in carcass weight resulting in relatively poor economic gains.

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CHAPTER ONE

INTRODUCTION

Beef cattle have a number of roles in developing countries such as Indonesia. They have been posted as an important natural resource in livestock development activities in order to increase farmer income, create job opportunities, supply manure for fertilizing household farming and in particular to provide domestic meat demands (Kartamiharja, 1987). As Indonesia has about 4 million ha of unutilized land which is suitable for grazing ruminants (Anonymous, 1987), the option is open to increase the beef cattle population and hence beef production by means of extensive farming systems (Kasryno et al., 1987). However, beef production developments are limited by the native unimproved beef cattle (Anonymous, 1984). To overcome this problem and to provide future roles for beef cattle, animal breeding is a necessary component to improve beef cattle productivity (Cartwright and Blackburn, 1989).

Livestock improvement programs in the tropic regions should include the native genetic resources which may have been well adapted to stresses of the environment (Fitzhugh, 1990 and Vercoe and Frisch, 1990). Among Indonesian indigenous beef cattle, for example, Madura cattle, Sumba Ongole cattle and Bali cattle (Hardjosubroto and Astuti, 1980 and Pane, 1986), Bali cattle have been identified as high priority for further improvement (Pane and Packard, 1987). This is reasonable because Bali beef cattle have an important socio-economic role for farmers, ability to thrive under poor conditions, high dressing percentage, high fertility and low fat content (Payne and Rollinson, 1973, Subandryo et al., 1979 and Hardjosubroto and Astuti, 1980). Since 1982 attempts have been directed to systematically improve Bali beef cattle.

Planning a beef cattle breeding program involves various steps, for example, describe the production systems, formulate the objective, choose a breeding system, estimate genetic parameters and economic weights, design an evaluation method, develop selection criteria and choose a mating system (Harris *et al.*, 1984 and Ponzoni, 1988a). In describing production systems, it should be realized that an individual is a unit of the production system and it may interact with the environment so all inputs and outputs of the system must be simultaneously considered to evaluate the contribution of an individual (Cartwright, 1979). Considering the breeding objective which is a crucial step in a breeding program (Ponzoni, 1988a and Johnson and Garrick, 1990), the main goal is to improve the overall net profit of the commercial farmers (Cartwright, 1982 and Blair, 1989). The beef cattle breed chosen is expected to produce desirable economic traits, for example, low maintenance (smaller size of cows), high fertility, good milking ability, efficient growth (fast growth) and high killing percentage with a preferable carcass grade (Cartwright, 1982). All of the desirable traits which will be improved through the breeding program, are required to have available estimates of genetic and phenotypic parameters as well as economic weights, as these are not only used to predict responses to selection but also to identify the selection criteria (Harris *et al.*, 1984). The need of selection criteria is because not all traits can be measured before making any decision to select or cull animals being evaluated.

Ideally, phenotypic and genetic parameters that will be implemented in an animal improvement program should be derived from the same breed and environment in which selection is to occur. These parameters and economic weights of each trait in the selection objective can then be formulated into an index, through which maximum responses in genetic improvement are to be reached in order to attain the overall selection objective. As a consequence, the need of phenotypic and genetic parameters as well as the economic weights is urgent for formulating a selection index when designing a long term genetic improvement program.

It should be noted that the limitation of knowledge of genetic parameters is the main factor affecting genetic selection programs (Subandryo *et al.*, 1970, Pearson, 1982, Vaccaro *et al.*, 1988 and Simm *et al.*, 1990). For the long term breeding program of Bali beef cattle, required parameters should be based on the Bali beef cattle. However, there are no available parameters and any effort to estimate parameters for Bali beef cattle should now be thought of as a valuable step.

The purposes of the present study are to estimate phenotypic and genetic parameters for weaning and yearling weight of Bali cattle. These parameters will be used to derive a selection index to be incorporated into a selection program.

CHAPTER TWO

REVIEW OF LITERATURE

2.1. INTRODUCTION

From the genetic improvement point of view, response to selection in terms of genetic gain per year (R) should be a crucial point of programs whether the selection objective is through a single trait or for multiple traits. It depends on selection intensity (i), correlation between the clue, C, and the true breeding value, A, (r_{AC}), standard deviation of additive genetic variance (σ_A) and generation interval (L) and it can then be expressed as follows :

$$R = [(i)\,(r_{AC})\,(\sigma_A)] / L$$

The correlation between the clue and the true breeding value (r_{AC}) is determined by factors such as the number of measurements per animal, the source of performance and the number of traits being selected as it is shown in table 2.1. From table 2.1, it is clear that parameters such as heritability (h^2), additive genetic variance (σ^2_A), phenotypic variance (σ^2_P), additive genetic covariance ($\sigma_{Ax,y}$) and phenotypic covariance ($\sigma_{Px,y}$) between traits (that is trait x and y) are urgent requirements when the genetic value (breeding value) and the response of selection are to be estimated. To obtain these parameters, it is important to emphasize that adjusting data for known non-genetic effects, that is environmental effects which can be readily identified, allows a more valid genetic value to be obtained. Therefore, identifying environmental factors which may significantly contribute to a beef trait performance is useful.

The first part of the present chapter will discuss non-genetic effects on beef cattle growth traits. Other parts describe several methods to generate variance and covariance components which are needed to estimate phenotypic and genetic parameters, and highlight results of previous studies involving phenotypic and genetic parameters of traits determining beef cattle productivity.

Table 2.1. Various values of correlation between the clues and the true breeding value (Van Vleck *et al.*, 1987).

Selection objectives	Source of information	Number of records	Value of r_{AC}
1.Single trait	**1.1. Own performance**	1	h
		n	$h \sqrt{[(n)] / [1 + (n-1)t]}$
			where t : repeatability
	1.2. Relatives only :		
	1.2.1. Average ancestors :		
	1.2.1.1. Sire and dam	1	$h (\sqrt{.5})$
		n	$h \sqrt{[.5 n] / [1 + (n-1) t]}$
	1.2.1.2. Four grandparents		$h (\sqrt{.25})$
	1.2.1.3. Eight g.grandparents		$h (\sqrt{.125})$
	1.2.2. Sibs only :		
	1.2.2.1. Half sibs	n records	$h \sqrt{[(.0625 n)] / [\{1 + (n-1).25 h^2\}]}$
	1.2.2.2. Full sibs	n records	$h \sqrt{[(.25 n)] / [\{1 + (n-1).5 h^2\}]}$
			where no common environmental effects exist
	1.2.3. Progeny only (n half-sibs)	n records	$h \sqrt{[(n)] / [4 + (n-1) h^2]}$
	1.3. Combination		
	1.3.1. Individual and one parent or progeny		$\sqrt{[5h^2 - 2h^4] / [4 - h^4]}$
	1.3.2. Individual and both parents		$\sqrt{h^2 [2h^2 - 3] / [h^4 - 2]}$
2. Multiple traits			$\sqrt{[b_1 a_{1\alpha} + ..., + b_k a_{k\alpha}]}$
			where **a** is the correlation between clues and the breeding value and the value of **b** (weighting factors) depend on and deriving from h^2, σ^2_A, σ^2_P, r_g and r_p

2.2. NON-GENETIC EFFECTS

2.2.1. Introduction

Differences in phenotype between animals are determined by their respective genetic and environmental (non-genetic) components. Non-genetic contributions to the phenotype are important for two reasons. Firstly, the magnitude of their effects on overall beef performance may enable development of more effective management systems to increase overall beef productivity. Secondly, the known non-genetic effects can be included in the analysis to derive a more accurate evaluation of genotype.

This sub-chapter will discuss the non-genetic effects that may influence beef productivity. Discussion of non-genetic effects will be only focused on beef cattle body weights as they have moderate to high phenotypic and genetic correlations with carcass traits such as carcass weight, dressing percentage and fat thickness and with reproduction traits such as scrotal circumference, age and weight of puberty and calving ease. They are herd, year and season or month of birth, age of dam, sex and age of calf and possible significant interactions among them.

2.2.2. Non-genetic aspects

2.2.2.1. Herd

Herd has been well known as having significant effects on the birth weight of beef cattle (Vesely and Robison, 1971, Chapman *et al.*, 1972 and Baker *et al.*, 1974). Trail *et al.* (1985) noted that the region of the ranch had a significant effect on birth weight of Boran cattle maintained under trypanosomiosis risk due to unequal treatment application. McKay *et al.* (1990) reported that the location influenced significantly birth weight of various beef cattle breeds due to differences in given management. However, Tewolde (1988) observed that herd, in terms of management system, was not an important source of variation for birth weight of

Romosinuano cattle in Latin American tropics. Differences of prenatal maternal influences due to different management among herd or regions on pregnant cows is the possible explanation of significant effects of herd on birth weight of beef cattle.

Results of studies also indicate that herds have significant effects on weaning weight of beef cattle (Vesely and Robison 1971, Chapman *et al.*, 1972, Martojo, 1975 and Nicoll and Rae, 1977, Cardelino and Castrol, 1988 and Rosa *et al.*, 1988). Dealing with data collecting from various regions, Anderson and Wilham (1978) found that weaning weights of Angus calves were statistically different between regions due to management applied. Crow and Howell (1982) found that approximately 50% of the variation in weaning weights of Angus, Charolais and Hereford performance was due to herd-year effects. Trail *et al.* (1985) noted that region of the ranch had significant effects on cow productivity of Boran cattle maintained under trypanosomiosis risk as resulting from different given treatments.

Herd may still have significant effects on post-weaning growth traits (Tallis, 1989), yearling and post-yearling weight of beef cattle (Rosa *et al.*, 1988 and Oliveira and Duarte, 1989). Kennedy and Henderson (1975a) found herd differences to account for 25 to 44% of total variation for growth traits (weaning weight, yearling weight and post-weaning gain). Nicoll and Rae (1978) noted that the most important single source of variation of 18 month weight within breed and sex was the herd effect.

In summary, significant herd effects on production traits may reflect differences in the genetic potential for growth capability in the calves and / or differences in management and given feeding levels. From a genetic point of view, if herd has a significant effect on growth traits, animals should be genetically ranked within herds, unless a sire referencing scheme is undertaken.

2.2.2.2. Year of birth

Year of birth has significant effects on beef cattle birth weight (Vesely and Robison, 1971, Baker *et al.*, 1974, Hernandez, 1977, Ahunu and Makarenchia,

1986, Wilson *et al.*, 1986, Rosa *et al.*, 1988, Tewolde, 1988, DeNise *et al.*, 1988, Tawonezvi, 1989a and Buvanendran, 1990). Dealing with field records of Hereford cattle, Itulya *et al.* (1987) found that there was a large variation in birth weight between year of birth. However, some studies reported that there were no significant effects of year of birth on birth weight of beef cattle (Duarte *et al.*, 1986 and Bailey and Lawson, 1986). In general, the effect of annual fluctuations of feed available on prenatal maternal environments is likely to be the main reason of effects of year of birth on beef cattle birth weight.

Year of birth has also been noted having significant effects on beef cattle weaning weights (Singth *et al.*, 1970, Martojo, 1975, Nicoll and Rae, 1977, Pabst *et al.*, 1977, Ahunu and Makarenchia, 1986, Itulya *et al.*, 1987, Tewolde, 1988, Rosa *et al.*, 1988, Tawonezvi, 1989a, Dinkel, 1990 and Lubout and Swanepoel, 1990). It may contribute the greatest proportion of variation in weaning weight (DeNise *et al.*, 1988).

Year of birth may still have important influences on beef cattle post-weaning weight (Chapman *et al.*, 1972, Baker *et al.*, 1974, Nicoll and Rae, 1978, Cardellino, 1988 and DeNise *et al.*, 1989) and post-yearling weight (Sharma *et al.*, 1982, Rosa *et al.*, 1988, Oliveira and Duarte, 1989, Kim *et al.*, 1988, Tawonezwi, 1989a and Lubout and Swanepoel, 1990). Tewolde (1988) observed that weights at 18-month and 24-month of Romosinuano cattle in Latin American Tropics was significantly affected by year of birth as an indication of the influence of environmental fluctuations.

In summary, different quality and quantity of forage available due to annual climatic variation is likely to be the main cause of the effect of year on beef growth traits. Genetic trend may also contribute to the year effect. The year in which an animal is born fixes the set of environments to which it will be dependent. Consequently, animals born in different years will share non-identical environments. From the genetic point of view, it may not be necessary to adjust

for the effect of year of birth if the selection of animals is based on year contemporary groups.

2.2.2.3. Season of birth

Season of birth may significantly influence the beef cattle birth weight (Ordonez *et al.*, 1984, Trail *et al.*, 1985, Duarte *et al.*, 1986, Hoogesteijn *et al.*, 1987, Cardelino and Castro, 1988, Rosa *et al.*, 1988 and Winroth, 1990). The combined influence of calving year and season of birth was shown to account for 49.6% and 63.7% of the variation in weight at 4 months in Hereford and Angus, respectively (Brown *et al.*, 1972). In general, different feed quality and quantity available among seasons for pregnant dams is a possible explanation of effects of season of birth on calf birth weight.

Season or month of birth may significantly affect beef cattle weaning weight (Brown, 1960, Cundiff *et al.*, 1966, Cardelino and Castrol, 1988 and Rosa *et al.*, 1988). Trail *et al.* (1985) found that weaning weights of crossbred beef cattle in Uganda region were significantly affected by season of calving due to seasonal fluctuations of pasture available. Dealing with Mashona cattle, Buvanendran (1990) reported month of birth contributed 2% of the weaning weight variation. It was also observed to significantly affected yearling weight (Tewolde, 1988, Presinger and Kalm, 1988, Rosa *et al.*, 1988 and Oliveira and Duarte, 1989) and post-yearling weight (Ordonez *et al.*, 1984).

Influences of year and season of calving on calf growth depends on the age of the calf itself. The influence of calving year and season of birth decreased rapidly to less than 30 % at 12 months and less than 6% at 36 months (Brown *et al.*, 1972). Brown *et al.*, (1972) noted that a lack of a significant effect of month of birth on post-yearling weight indicated that compensatory growth had occurred so calves born in autumn or summer had caught up with the spring born-calves. Pabst *et al.* (1977) found that month of birth was a significant source of variation on 400-day weights of Hereford and Aberdeen-Angus breed but not for Charolais and Devon.

Differences in post-weaning growth due to different season of birth could be traced back to the conditions such as cows' feeding status and calf ability to utilize the milk and grazing available (Els and Venter, 1990).

In summary, fluctuations of feed supply due to seasonal rainfall and the ability of calves to utilize feed available are the main possible explanation of effects of season of birth on growth performance. This non-genetic effect should be considered when evaluating animals genetically, especially in systems where calving occurs throughout the year.

2.2.2.4. Age of dam

A number of studies recognized that age of dam had significant effects on birth weight of beef cattle (Smith *et al.*, 1976, Gregory *et al.*, 1978, Duarte *et al.*, 1986, Tewolde, 1988 and Burrow *et al.*, 1991). Vesely and Robinson (1971) noted that birth weight increased with increasing age of dam until about 8 years. Ahunu and Makarechian (1986) observed that birth weights increased significantly with the increase in age of dam up to 4 years in beef crossbred animals and 5 years in a Hereford population. Tawonezvi (1989a) found that birth weight of Mashona cattle increased with the increasing age of dam to 7 years. It seems that the cows with age between 4- to 8- years old produce higher birth weights than other age groups. The maturity of cows which determines the prenatal maternal influences on calf during pregnancy period is the main possible factor affecting birth weight.

Age of dam had also significant effects on weaning weight of beef cattle (Rhodes *et al.*, 1970, Rutledge *et al.*, 1971, Smith *et al.*, 1976, Gregory *et al.*, 1978, Nicoll and Rae, 1977, Nicoll and Rae, 1978, Anderson and Wilham, 1978, Leington *et al.*, 1982, Butzon *et al.*, 1980, Elzo *et al.*, 1987, Cardellino, 1988 and Burrow *et al.*, 1991). In a study in Mashona cattle, Buvanendran (1990) reported age of dam had significant effects on weaning weight and controlled about 5.4 % of total variation.

Increasing age of dam may differently affect weaning weight depending on the degree of dam maturity. Singth *et al.* (1970) found that the effect on calf weaning weight of Hereford cattle was greater from cows 5 to 7 years old and less from 4 year old cows. Nelson *et al.* (1970) in a study of factors affecting weaning weight of *Bos indicus* in Paraguay found that peak production for Santa Getrudis x Criolla cows was between 6- to 8-years of age while 4- and 10-year-old cows generally produced lighter calves. Another study indicated that weaning weight increased with increasing age of dam of Hereford cattle until about 8 years (Vesely and Robison, 1971). Pabst *et al.* (1977) showed that calves from 2 year-old dams had 200-day weights 5% to 11% lower and calves out of 3 year-old dams 2% to 9% lower than calves from 5 to 8 year-old dams. Anderson and Wilham, (1978) found that the weaning weight of Angus calves increased as cows matured and declined after cows reached between 6 and 9 years of age. From various results of studies, there appears that maximum weaning weight of beef calves will be attained when dams are approximately 5 to 9 years old.

The effect of age of dam on productivity reflects maturity such as development of the mammary gland, milk yield and maternal ability. Maternal influences in terms of the ability to produce milk is the main factor of effects of cow age on weaning weight (Rutledge *et al.*, 1971 and Notter *et al.*, 1978). Neville (1962) noted that 66% of the total variation in 8- month calf weight was attributable to differences in milk consumption. Jeffery *et al.* (1971) confirmed that milk yield had the greatest influence on pre-weaning performance explaining about 60% of variation in average daily gain and 40% to 50 % of the variation in weaning weight. Since age of dam had a quadratic effect on milk yield with a maximum occurring at 8.4 years (Rutledge *et al.*, 1971), it is reasonable that cows at approximately this age have better mothering ability than either older or younger cows. This can be explained by young cows still having a nutritive requirement for growth, while for old cows may have a poorer ability to cope with nutritional and other environmental stress factors (Trail *et al.*, 1985).

Age of dam may still affect the post-weaning weight and gain of beef calves (Bair *et al.*, 1972, Young *et al.*, 1978 and DeNise and Torabi, 1989), yearling weight (Sharma *et al.*, 1982, Rosa *et al.*, 1988 and Oliveira and Duarte, 1989) and post-yearling weight (Nicoll and Rae, 1978 and Raymond *et al.*, 1980). Tewolde (1988) reported that age of dam was important (P < .01) in describing post-weaning growth on pasture of Romosinuano cattle in Latin American tropics due to the possibility of a carryover effect of pre-weaning maternal environment that calves were subjected to during their pre-weaning growth.

Effects of age of dam on growth rate decline as calves grow older (Brown *et al.*, 1972, Pabst *et al.*, 1977, Bean and Seifert, 1979 and Seifert *et al.*, 1980) but may still remain important through to 18 - 20 months of age (Baker *et al.*, 1974, Seifert *et al.*, 1980 and DeNise *et al.*, 1989). However, Raymond *et al.* (1980) indicated that by 550 days the influence of dam age was negligible for Angus heifers under Australian conditions. Some studies found that age of dam had no significant effects on post-weaning gain (Rudder *et al.*, 1975 and Tawonezvi, 1989a), yearling weight (Planas, 1987 and Kim *et al.*, 1988) and post-yearling weight of beef cattle (Kim *et al.*, 1988 and Tawonezvi, 1989a).

The effect of age of dam on post-weaning weight is a further consequence of environmental effects of the dam on her calf during pregnancy and pre-weaning period. If a dam supplies her calf an adequate environment during the pre-weaning growth stage, then the calf post-weaning growth may depend only on the ability of the calf to grow. Inadequate pre-weaning environments may lead to post-weaning compensatory growth (Elzo *et al.*, 1987).

In summary, age of the dam has significant effects on birth, pre-weaning and weaning weight due to the direct maternal influence on calf performance. The effect of age of dam on post-weaning growth is due to a carryover of maternal effects. Effects of age of dam on calf growth performance depend on the dam's maturity age (reflecting the conflict of physiological and physical ability) and the

age of the calf (decreases with increasing age of the calf). Therefore, for genetic purposes, adjustment factors for age of dam should account for each stage of growth.

2.2.2.5. Calf sex

Several studies have indicated that calf sex had significant effects on birth weight (Vesely and Robinson, 1971, Trail *et al.*, 1985, Sharma *et al.*, 1982, Ahunu and Makarechian, 1986, Tewolde,1988, Els and Venter, 1990, Lubout and Swanepoel, 1990, Naves and Vallee, 1990, Winroth, 1990 and Burrow *et al.*, 1991). Pabst *et al.* (1977) noted that sex was the greatest source of variation in calf birth weight and that differences due to sex tended to increase with the size of the breed.

Calf sex also had significant effects on weaning weight (Sharma *et al.*, 1982, Trail *et al.*, 1985, Ahunu and Makarechian, 1986, Naves and Vallee, 1990 and Burrow *et al.*, 1991) and made the greatest contribution to variation in weaning weights (Jeffery *et al.*, 1971, Pabst *et al.*, 1977, Leington *et al.*, 1982 and Buvanendran, 1990). In conditions where management was the same for both sexes, Koch *et al.* (1973) showed that pre-weaning daily gain of bulls was 7% to 8 % higher than for heifers. Plasse (1978) in a summary of effects of sex on body weight of *Bos indicus* noted that in general males had 7% to 11 % higher weaning weight than for females. Dealing with various breeds of *Bos taurus*, Winroth (1990) observed that heifers had a relative weight at weaning of 89-92% of that of bulls.

Studies have also shown that sex of calves had significant effects on post-weaning weight (Singth *et al.*, 1970, Rodhes *et al.*, 1970, Baker *et al.*, 1974, Nicoll and Rae, 1977, Nicoll and Rae, 1978, Anderson and Wilham, 1978 and Tonhati *et al.*, 1986), yearling weight (Winroth, 1990) and post-yearling weight of beef cattle (Tewolde, 1988 and Burrow *et al.*, 1991). The relative importance of sex of calves tends to increase with age (Pabst *et al.*, 1977 and Tewolde, 1988) and it may contribute the greatest source of variation in body weight variation (Tewolde, 1988).

In summary, sex of calf is one of the most important non-genetic factors influencing growth performance of beef cattle. It appears that the sex differences in physiological and hormonal activity on growth mechanism is a possible explanation for significant effects of sex on production traits. Males calves are heavier at birth and weaning and grow faster than females calves. Therefore, ranking animals based on sex contemporary group is a more accurate method in genetic point of view.

2.2.2.6. *Age of calves*

Various studies have indicated that the growth rate of beef calves tends to be linear from birth until weaning ages. Most studies observed that age at weaning had a significant effect on weaning weight (Singth *et al.*, 1970, Jeffery *et al.*, 1971, Baker *et al.*, 1974, Nicoll and Rae, 1977, Barlow and Dettman, 1978, Butson *et al.*, 1980 and Buvanendran, 1990).

Age at weighing also has a significant effect on post-weaning weight. Results of studies reported that effect of age on body weight was different between sex of calf ((Pabst *et al.*, 1977 and Tewolde, 1988). Swiger *et al.* (1963) illustrated that bulls would reach a maximal growth rate after about one year of age while that for heifers occur after weaning. Rhodes *et al.* (1970) observed that there was a negative quadratic value obtained for age of calves which indicated that the rate of weight increase declined with increasing age. Other studies also showed that the regression of weight on age of calves was the most single source of variation of body weight and this contribution also declined proportionately as the calves grew older (Baker *et al.*, 1974, Nicoll and Rae, 1977 and Nicoll and Rae, 1978). However, Presinger and Kalm (1988) observed that the quadratic regression of weight on age at 200 day and yearling was not significant for Charolais field data.

In summary, it appears that age at weighing has important effects on production traits. A regression method is suggested for adjustments as it is a continuous effect. Since its effects will decrease with increasing age of calves and depend on

the growth pattern of beef breeds, preliminary analysis should be taken to examine whether its effect is linear or quadratic on production traits.

2.2.2.7. *Interactions*

Interactions among non-genetic effects (herd, year, season, dam age group and calf sex) may contribute important variation to growth traits of beef cattle.

Herd by year of birth interactions have been noted to have significant effects on beef cattle birth weight (Chapman *et al.*, 1972), weaning weight (Chapman *et al.*, 1972 and Martojo, 1975) and post-yearling weight (Nicoll and Rae, 1978). Trail *et al.* (1985) showed significant interactions between the region of the ranch and year for traits such as birth weight and weaning weight of Boran cattle. In general, significant herd by year interaction may be due to differential management and variation of feed available among years.

Herd by season of birth interactions may be important sources of variation on beef cattle growth traits. Cundiff *et al.* (1966) in a study on Hereford and Angus cattle observed that season of birth by pasture and management interaction was important for weaning weight variation due to the different type of pasture utilized at the month of birth. Trail *et al.* (1985) found significant interaction effects between the region of the ranch and season of birth for traits such as birth weight and weaning weight of Boran cattle which were presumably due to different seasonal rainfall among areas. In general, difference in seasonal feed supply due to different seasonal rainfall and different management is the main explanation of significant interaction between herd and season of birth.

Beef cattle growth traits may be influenced by the existence of herd by age of dam interaction. Schaefer and Wilton (1974) reported that there was evidence of significant effects of interaction between feeding system by age of dam on weaning weight of Angus and Hereford herds. McKay *et al.* (1990) found significant effects of age of dam by location interaction on pre-weaning daily gain and

weaning weight of various beef breeds due to different conditions experienced by the cows during lactation. However, other studies reported that herd by age of dam interaction had no significant on birth weight (McKay *et al.*, 1990) and weaning weight (Cundiff *et al.*, 1966 and Baker *et al.*, 1974). In general, the presence of herd by age of dam interaction may be due to the different ability of each age group and breed of dam to respond to any given feeding and management level. On some farms, age classes may be run separately and given different management, leading to an interactions.

Significant interaction effects may exist between herd and sex of calf influencing beef cattle birth weight (Cardellino and Castro, 1988), preweaning traits (DeNise *et al.*, 1988) and weaning weight (Martojo, 1975). Rhodes *et al.* (1970) observed that management by sex interaction effects on weaning weight of Angus and Hereford calves indicated that differences among sexes were not consistent for creep and non-creep fed calves. However, some studies indicate that there were no significant interaction effects between herd and sex on birth and weaning weight (Chapman *et al.*, 1972). In general, significant herd by sex interaction effects may be due to difference of physiological and hormonal mechanisms among sex to respond on any given management, especially feed supply.

There have been reports of significant year by month of birth interaction effects on beef growth traits, for example, on birth weight (Hoogesteijn *et al.*, 1987), weaning weight (Cardellino and Castro 1988 and Rosa *et al.*, 1988) and on post-yearling weight (Rosa *et al.*, 1988). However, other studies have shown no significant interaction effects between year and month of birth on beef cattle body weights under some conditions, for example, that on weaning weight of Mashona cattle in Zimbabwe (Buvanendran, 1990) and on birth weight and weaning weight of Limousin in Sweden (Winroth, 1990). In general, seasonal and yearly fluctuations of feed available due to different distributions of rainfall is the most likely factor causing significant year by month interaction effects on production traits.

Significant interactions on production traits may exist between year and dam age at calving (Baker *et al.*, 1974 and Nicoll and Rae, 1978). Buvanendran (1990) in a study with Mashona cattle in Zimbabwe, reported that the significant year of birth by age of dam interaction effect accounted for about 2% of the variation in weaning weight. Significant year by age of dam interactions may reflect the difference in nutritional requirements due to a dissimilarity in physiological maturity and physical ability of the cows to utilize available forage (Itulya *et al.*, 1987). Therefore, years that were best for young cows did not seem to best for older cows.

The interaction between year of birth and sex of calf may significantly influence beef cattle birth weight (Tewolde, 1988), weaning weight (Srinivasan and Martin, 1970, Baker *et al.*, 1974 and Buvanendran, 1990), post-weaning growth (Tewolde, 1988) and post-yearling growth (Tewolde, 1988). Ahunu and Makarenchia (1986) reported that the year by sex of calf interaction was significant for birth weight and weaning weight for synthetic and crossbred beef cattle due to the relative superiority of males to females in gradually improved environments. However, other studies noted that year by sex of calf interaction was not significant for birth weight of Herefords (Ahunu and Makarenchia, 1986), weaning weight of Herefords (Martojo, 1975, Ahunu and Makarenchia (1986), Angus and Brahman cattle (Martojo, 1975). In general, year of birth by sex of calf interaction effects on production traits may be due to the relative superiority of males compared to females to utilize available food which may fluctuate annually depending on annual rainfall distributions.

Cundiff *et al.* (1966) reported a small interaction between season of birth and age of dam relative to other non-genetic effects on weaning weight of Hereford and Angus cattle. In a study with Mashona cattle, Buvanendran (1990) found a non-significant season of birth by age of dam interaction on weaning weight. These studies indicate that the effect of age of dam is essentially the same regardless of season of birth. However, if there is significant interaction between season of birth

and age of dam on calf growth traits, the effect of age of dam will be different among season of birth contemporary groups. A significant interaction between season of birth and age of dam on growth traits of calves especially at the pre-weaning stage, may indicate the seasonal variation of feed supply and different maternal influences among dam age groups as resulting of different ability to utilize available food.

Season of birth by sex of calf interactions have been reported to have significant effects on beef cattle growth traits, for example, pre-weaning gain (Ledic et al., 1987 and Cardellino and Castro, 1988). However, other studies indicated that there was no significant month of birth by sex interactions on weaning weight of beef cattle (Cundiff et al., 1966 and Buvanendran, 1990). In general, a possible explanation of the significant month of birth by sex interaction on growth traits is the seasonal variation of feed supply due to seasonal rainfall distribution and different ability of each sex and stage of growth contemporary group to find and then utilize available pasture.

Dam age by sex of calf interaction may significantly affect beef cattle birth weight (Aaron et al., 1987) and weaning weights (Martojo, 1975, Baker et al., 1974, Anderson and Wilham, 1978 and Sharma et al., 1982). However, other studies observed that there was no significant interaction between the age of dam and sex of calf for birth weight (Baker et al., 1974, Ahunu and Makarechian, 1986 and McKay et al., 1990), weaning weight (Cunningham and Henderson, 1965, Nicoll and Rae, 1977, Buvanendran, 1990 and McKay et al., 1990) and post-weaning weight (Baker et al., 1974 and Tewolde, 1988). Cundiff et al. (1966) noted that heifer calves from 2- and 8-year old cows deviated significantly less from their mean than did bull calves due to a possible tendency of male calves to challenge their dams more and stimulate more milk flow than heifer calves. In general, significant age of dam by sex interaction effects on calf growth traits reflect different levels of milk production among dam age groups due to differential stimulation by male versus female calves.

2.2.3. Conclusion

The above discussion shows that non-genetic effects alone (herd, year of birth, season of birth, age of dam, sex and age of calf) or interactions among them often exhibit significant effects on weight and growth traits of beef cattle. These effects should be accounted for when attempting to rank animals based on their genotype, thereby increasing the accuracy of selection and enhancing the rate of genetic gain. The adjustment of traits for non-genetic effects can be undertaken using predermined adjustment factors or by fitting a linear model containing the non-genetic effects to each data set, providing there are sufficient numbers of observations.

2.3. METHODOLOGY FOR DERIVING VARIANCE COMPONENT ESTIMATES

2.3.1. Introduction

Animal breeding studies frequently deal with unbalanced data and involve mixed linear models, that is, linear models including fixed effects (when inferences only represent effects that occur in data) and random effects (when inferences from a set of effects can be larger than those that occur in the data) (Anderson, 1984).

Whilst estimation of variance and covariance components in mixed models with balanced data, that is with equal numbers of observations in the sub-classes, is straightforward (by equating the mean square to their expectations), estimating of those in mixed models with unbalanced data often requires complex statistics. This problem has encouraged attempts to investigate a variety of methods for estimating variance and covariance components from either unbalanced experimental or field data.

It has been well known that the paper of Henderson (1953) is a significant highlight of methods for estimating variance components from unbalanced data.

These methods have become known as Henderson's Methods (Method I, II and III). Other methods include maximum likelihood (ML) which was first presented by Hartley and Rao (1967), restricted maximum likelihood (REML) that was suggested by Patterson and Thompson (1971), minimum norm quadratic unbiased estimation (MINQUE) and minimum variance quadratic unbiased estimation (MIVQUE). For the researcher, it may be difficult to select a technique for any given data set. Therefore, efforts to understand their derivations, relationships, merits and demerits for any particular set of conditions may be helpful before selecting a method and utilizing it to estimate variance and covariance components.

This section will briefly review some methods for estimating variance components, primarily from unbalanced data. Discussion will emphasize model derivations, relationships, merits and demerits.

2.3.2. Methods

2.3.2.1. Henderson's Methods

2.3.2.1.1. Introduction

The three Henderson's Methods of estimating variance components are methods that can be used on unbalanced data when more than one factor occurs in the model (Henderson, 1953). The procedures such as setting up normal equations, computing reductions in sum of squares due to fitting parameters in the models and then equating results of the reductions to corresponding expected values, are basic principles of Henderson's Methods for estimating variance components (Anderson, 1984). Each of the methods is an application of the Analysis of Variance (ANOVA) methodology, although they are judicious and ingenious applications (Searle, 1989). They differ only through the different sets of quadratic forms.

2.3.2.1.2. Henderson's Method I

Originally, Henderson's Method I was discussed by Cochran (1939) with the additional specification that it is only applicable in the case of random models

(Anderson, 1984). It uses quadratic forms that are adaptations of sum of squares used as for balanced data so it is often known as the ANOVA method (Searle, 1971). From Anderson (1984), a general form of the model for which the Henderson's Method I is appropriate is :

$$y = 1\mu + \sum_{i=1}^{k-1} Z_i u_i + e \qquad (1)$$

where :

y = an N x 1 vector of observations,

1 = a N x 1 vector,

μ = an unknown vector of general mean,

Z_i = N x c_i known matrices, i = 1, 2, ..., k-1, and

u_i = non-observable vectors of random effects of order c_i x 1, i = 1,

     2, ..., k-1.

e = a vector of N x 1 of error terms due to y observations.

This model will be valid under assumptions (i) $E(u_i) = 0$, i = 1, 2, ..., k and (ii) the elements of u_i are independently distributed with common variance σ^2_i and kurtosis $\ddot{y}_i$, where $\ddot{y}_i = E (\mu^4_{ij}) / (\sigma^4_i - 3)$, for j = 1, ..., c_i and (iii) μ_i and μ_i' are independent for i ≠ i'. The error terms are assumed to be independently and identically distributed with mean zero and variance σ^2_e. The vector of observations, y, has:

$$E(y) \quad = 1\mu \text{ and}$$

$$var(y) \quad = \sum_{i=1}^{k-1} \sigma^2_i V_i = V, \text{ where} : V_i = Z_i Z_i'.$$

To generate variance component estimates, Henderson's Method I exploits reductions in sums of squares by fitting each random effect, $R(u_i)$, plus a reduction due to fitting the mean, $R(\mu)$, in the linear model (1). These reductions are to be calculated by :

$$R(\mu) = y'1 (1'1)^{-1} 1'y$$

$$R(\mu) = y' 1 1' y / N \text{ and}$$

$$R(u_i) = y'Z_i (Z_i'Z_i)^{-1} Z_i'y,$$

for i = 1, ..., k-1, while the total sum of squares is expressed by $y'y$.

By equating the reduction of sum of squares due to fitting the mean and the random effects in the model to their expected values, the variance components for residual (σ^2_e) and random effects ($\sigma^2 u_i$) can then be estimated as follows :

$$\hat{\sigma}^2_e = [\, y'y - R(u_i) \,] \, / \, [N - a] \, ,$$

$$\hat{\sigma}^2 u_i = [\, \{R(u_i) - (R(\mu)\} \, / \, \{(a-1)\} - \hat{\sigma}^2_e] \, / \, k_1 \, ,$$

where:
$$k_1 = [\, \{N - (\, \sum_{i=1}^{a} n^2_i \, / \, N)\} \,] , \text{ and}$$

$$a = k-1.$$

The main merit of the Henderson's Method I is its ease of calculation so it is especially suitable in conditions where modern computers are unavailable (Searle, 1978, Searle, 1989). In conditions where a random model is appropriate, Henderson's Method I is a possible method for estimating variance components as it yields unbiased estimates. However, the Method I can not be used for mixed models. Searle (1989) pointed that the quadratic form used in the Henderson's Method I were such that for mixed models so it was defined to have a non-zero value. Whereas for random models the quadratic forms used such that to have a zero value. Although it is used for mixed models by assuming the fixed effects are random or by ignoring the fixed effects, it yields biased estimators of the variance components as they cannot be eliminated from the expectation used in the Method I. Additionally, Henderson Method's I may yield negative estimates of variance components as the reduction in sum of squares is not of positive definite form (Searle, 1978).

2.3.2.1.3. Henderson's Method II

Henderson (1953) showed that as the Method I was not suitable for a mixed model, Henderson's Method II was an alternative techniques. A general form of the appropriate mixed model of Henderson's Method II is :

$$y = X\beta + Zu + e \qquad (2)$$

where :

y = an N x 1 vector of observations,

X = a known matrix of order N x p,

β = a vector of p unknown and unobservable fixed effects,

Z = a known matrix of order N x i (i = 1, 2, ..., k),

u = a vector of order c_i (i = 1, 2, ..., k) of non-observable random effects, and

e = a vector of N x 1 of error terms due to y observations with assumptions as in equation 1.

Normal equation of model 2 can be written as follows :

$$\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z \end{bmatrix} \begin{bmatrix} \beta^{\circ} \\ u^{\circ} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix} \qquad (3)$$

Henderson's Method II involves steps such as obtaining a particular form of least squares estimates of the fixed effects in the model, that is β°, adjusting the data according to these estimates, that is use β° such that $z = y - X\beta^{\circ}$ and then applying Henderson's Method I to the adjusted data to estimate the variance components. Therefore, Method II is basically Method I with y replaced by $y - X\beta^{\circ}$ in all quadratic forms, both in the computation and in the taking of expected value.

The computations for Henderson's Method II are as easy as that for Method I. However, like Henderson's Method I, Method II may still yield negative estimates of variance components (Searle, 1989). Although Henderson's Method II can accommodate mixed models, it can not handle conditions involving interactions between fixed and random factors, nesting of fixed and random effects within each other or confounding between fixed and random effects (Anderson, 1984). Furthermore, the analytical expressions for sampling variances of estimators are not available.

2.3.2.1.4. Henderson's Method III

The general model and normal equations for Henderson's Method III are as shown in (2) and (3), respectively.

Henderson's Method III utilizes reductions in sum of squares obtained from fitting the full model and various different sub-models of it. It is also known as the Fitting Constant Method. This procedure generates reductions in sum of squares that are free of the fixed effects in the model. Following from normal equations (3), reductions of the sum of squares can be calculated by fitting the fixed effects and random effects based on the following equations :

$$R(\beta) \quad = y' \, X(X'X)^{-1} \, y$$

$$R(u|\beta) = \hat{u}'Z\{I - X(X'X)^{-} X\}y \,.$$

For animal breeding purposes where random effects in terms of genetic effects are of main interest, the expected value of the reduction in sum of squares due to fitting random effects after fitting fixed effects in the model, that is E [R(u|β)], is of central interest. It can be expressed as :

$$E\,[R(u|\beta)] \,=\, tr\,[\,Z'\{I - X(X'X)^{-}X'\}Z\,E(uu')] + \sigma^2 e\,[rank\,(X\,Z) - rank\,(X)]$$

Reductions in sum of squares are then equated to their expected values in order to yield variance component estimates. In general, variance component estimates ($\sigma^2 u$) can be generated from the following equations:

$$E\,R(u|\beta) = E\,(MSE + k_1\,\sigma^2 u)$$

where :
$$k_1 \quad = [\{\,N\ -(\textstyle\sum^k_{i=1} n^2_j\,/\,N\,)\,\}\,]\,,$$

so then :

$$\hat{\sigma}^2 u \,=\, [\,R(u|\beta) - MSE\,]\,/\,k_1 \,.$$

By contrast either to Method I, which cannot be used for mixed model at all, or to Method II, which is only suited to those mixed models that have no interactions between fixed and random effects, Henderson's Method III is a viable method for any mixed model. However, computing the reductions in sum of squares terms can require significant amounts of computer time. In some animal breeding situations which have large data sets, the method will deal with matrices of very large dimensions so it urges the use of very advanced computing facilities (Searle, 1989). This method is not uniquely defined as there can have more equations than variance components (Searle, 1978). Furthermore, as for Method I and II, Henderson's Method III may yield negative estimates of variance components.

2.3.2.1.5. Conclusion

In summary, Henderson's Methods yield unbiased estimators, they are translation invariant, especially Method II and III, and they do not require any distributional assumption about the data. However, they have a lack of uniqueness. With non-orthogonal data (e.g. unbalanced data), there are often more sum of squares to be computed than the variance components estimates required. Thus, the choice of different set of sum of squares will result in different estimates. These methods are also unable to generate best asymptotically normal estimates. Furthermore, none of them possess minimum sampling variance.

2.3.2.2. Maximum Likelihood (ML)

The estimation of variance components using ML method was developed by Hartley and Rao (1967). The procedure yields simultaneous estimations of both the fixed effects and the variance components by maximizing the likelihood concerned with respect to each element of fixed effects and with respect to each of the variance components.

Derivation of equations to examine a ML estimates of variance components can be based on the following mixed model (Anderson, 1984):

$$y = X\beta + \sum_{i=1}^{k} Z_i u_i \tag{4}$$

where:

y = an N x 1 vector of observations,

X = a known N x p matrices,

β = an known vector of p of fixed effects,

Z_i = an known N x c_i matrix, i = 1, ..., k, and

u_i = non- observable c_i x 1 vectors of random effects.

The model has a multi-variate normal distribution with means and common variance are $X\beta$ and V, respectively, where :

$$V = \sum_{i=1}^{k} \sigma^2_i V_i \text{ and } V_i = Z_i Z'_i \tag{5}$$

The logarithm of the corresponding likelihood function for the model equation (5) is :

$$L_y = -\tfrac{1}{2} N \log 2\Pi - \tfrac{1}{2} \log |V| - \tfrac{1}{2}(y - X\beta)'V^{-1}(y - X\beta) \tag{6}$$

Through differentiating L_y with respect to both β and σ^2_i and equating them to zero resulting in the following equation :

$$\{ tr(\hat{V}^{-1}V_i\hat{V}^{-1}V_j) \, \sigma^2 \} = \{ y' \hat{P} V_i \hat{P} y \}, i, j = 1, ..., k \tag{7}$$

where:

$$\hat{P} = \hat{V}^{-1} - \hat{V}^{-1}X (X' \hat{V}^{-1} X)^{-} X'\hat{V}^{-1} .$$

Maximum likelihood estimates of the variance components are then able to be yielded by solving the equation (7) iteratively with the constraint that the solutions $\sigma^2_i \geqslant 0, i = 1, ..., k$.

Maximum likelihood has the merit of simultaneously providing estimators of both the fixed effects and the variance components (Searle, 1989). Unlike ANOVA estimations, ML is able to be used to estimate variance components from

unbalanced data with random or mixed models (Searle, 1989). Another contrast is that ML estimators are always well-defined (numbers of mean squares yielded correspond to the number of variance components to be estimated) while Henderson's Methods are not well-defined as there are more mean squares from the ANOVA than there are variance components to be estimated (Harville, 1977). Unlike Henderson's Methods, ML, by its definition, yields non-negative variance components (Anderson, 1984). Harville (1977) noted that ML estimators were functions of sufficient statistic and are consistent and asymptotically normal and efficient.

However, there are a number of limitations of the ML method. ML equations for estimating variance components cannot be solved explicitly (Searle, 1971 and Searle, 1989) rather they require iterative procedures. Since ML results in sets of equations which will be iteratively solved, it needs large computational times (Harville, 1977 and Searle, 1989). To some extent, the recent advance of computing facilities has overcome this limitation. Another disadvantage of ML method for estimating variance components, particularly from a mixed model, is the bias from ignoring the loss in degrees of freedom due to fitting the model's fixed effects (Herville, 1977).

In summary, variance components estimated by the ML method has properties such as consistency, are asymptotically normal, always be functions of minimally sufficient statistics and by definition yielding non-negative variance components. However, ML has limitations, for example, requiring large computational times and facilities, ignoring the loss in degree of freedom due to fitting the fixed effects in the mixed model and yielding a downward bias of variance component estimates pertaining to any random effect with a small number of levels.

2.3.2.3. Restricted Maximum Likelihood (REML)

The Restricted Maximum Likelihood (REML) method was first suggested by Patterson and Thompson (1971). This method is a modification of the ML

procedure by dividing the likelihood under normality into two segments and then maximizing the segment which is independent of fixed effects (Corbeil and Searle, 1976a).

Derivation of equations to examine REML estimators of variance components can be approached through maximizing the likelihood associated with a set of, for example g, linearly independent error contrasts. From Anderson (1984), given an error contrast is a linear function of the observations, say $\mathbf{Ky}$, where $\mathbf{K}$ satisfies requirements such that $\mathbf{KX} = \mathbf{0}$, $\mathbf{KK'} = \mathbf{I}$, $\mathbf{K'K} = \mathbf{M} = [\mathbf{I} - \mathbf{X}(\mathbf{X'X})^{-}\mathbf{X'}]$ and $g = $ rank $(\mathbf{K}) = N - $ rank $(\mathbf{X})$ and the vector $\mathbf{Ky}$ ($\mathbf{y}$ from model 5) is normal distribution with means and variance are $\mathbf{0}$ and $\mathbf{KVK'}$, respectively, the logarithm of the likelihood function would be :

$$L_R = -\tfrac{1}{2} g \log 2\prod - \tfrac{1}{2} \log |\mathbf{KVK'}| - \tfrac{1}{2} \mathbf{y'K'}(\mathbf{KVK'})^{-1}\mathbf{Ky} \qquad (8)$$

By differenting L_R with respect to σ^2_i, equating them to zero and utilizing the fact that $\mathbf{PVP} = \mathbf{P}$, will produce the equation :

$$\{ \operatorname{tr}(\mathbf{PV_iPV_j}\} \, \sigma^2 = \{ \mathbf{y'PV_iPy}\} \qquad (9)$$

where $i = 1, ..., k$.

Restricted Maximum Likelihood estimates of the variance components are then able to be yielded by solving equation (9) iteratively with the constraint that the solutions $\sigma^2_i \geqslant 0$, $i = 1, ..., k$.

Dealing with balanced data, REML yields identical estimates as the ANOVA method does, including situations such as the 1-way model, the 2-way cross classification mixed model with and without interactions (Corbeil and Searle, 1976a). Another similarity between REML and Henderson's Methods is that both are based on equalizing translation-invariant quadratic forms to their expectation (Harville, 1977). However, with REML the quadratic forms are functions of the variance components while in Henderson's Methods they are functionally independent of the variance components. By contrast to Henderson's Methods where the expectations are linear and negative estimates of variance components

could be yielded, in REML, the expectations are non-linear and modifications are incorporated to account for non-negativity constraints (Harville, 1977). Moreover, Henderson's Methods are not well-defined as to which mean squares from the ANOVA should be used, while REML estimators are always well-defined (Harville, 1977).

REML eliminates the ML problem of being unable to handle the loss in degrees of freedom resulting from the model's fixed effects (Harville, 1977). Since REML is a further improvement of ML, it shares a number of ML properties such as only non-negative solutions are obtained, does not yield explicit estimators therefore requiring iterative procedures. Moreover, both REML and ML estimators of variance components are translation invariant (Corbeil and Searle, 1976b, Harville, 1977, Anderson, 1984). REML estimators are not only invariant to the fixed effects of the model but they are also free of the estimates of the fixed effects.

However, REML does not improve on ML in all properties. For instance, ML is still superior to REML in terms of minimally sufficient function (Harville, 1977). As for ML, REML estimates need costly computations to form and solve the numerous linear equations (Harville, 1977).

2.3.2.4.   *Minimum variance quadratic unbiased estimations (MIVQUE) and minimum norm quadratic unbiased estimations (MINQUE)*

Other methods for deriving variance components are minimum variance quadratic unbiased estimations (MIVQUE) and minimum norm quadratic unbiased estimations (MINQUE). MIVQUE has properties such as quadratic, translation invariant, unbiased estimators when the distribution is multi-variate normal and a minimum sampling variance of estimators (Henderson, 1986, Kennedy, 1989). However, MIVQUE has several undesirable properties such as negative estimates of some variances and for some situations there is an excessive requirement for computer capacity (Henderson, 1986). Under normality, estimators from MIVQUE are similar to those from REML. MINQUE is the first iterate from

REML. It has properties such as translation invariance and unbiasedness. In a balanced data case, estimators yielded by MINQUE are similar to those by ANOVA, Henderson's Methods and REML (Searle, 1978). For unbalanced data, estimators from MINQUE are similar to those from REML and MIVQUE if data normally distributed (Searle, 1978).

2.3.3. Conclusion

Following the previous discussion of several methods for estimating variance components, it is clear that, from an animal breeding point of view, the preference of any method for estimating the variance components depends totally on the given conditions and on the ease with which the method can be applied. For example, in order to handle unbalanced data where the appropriate model is the mixed model with interaction between fixed and random effects, and if there is a lack of advanced computational facilities, Henderson's Method III may be a preferred method rather than ML or REML.

2.4. PHENOTYPIC AND GENETIC PARAMETERS

This sub-chapter will discuss the various parameters such as heritabilities, phenotypic and genetic correlations among various beef cattle traits, required to formulate selection indices for ranking of animals based on estimated genetic merit.

2.4.1. Heritability

2.4.1.1. Introduction

The heritability of a character plays an important role in a genetic improvement program. Its magnitude can be used to estimate breeding values, to estimate the

response to selection in terms of genetic gain, to decide whether selection based on the individuals own performance is the appropriate method (if the value is high) or with its relatives (if the value is low) or to develop a selection index. Therefore the definition of heritability, factors that determine its value, methods to calculate it and which method yields the best estimate are useful concepts to know before reviewing various estimates that have been reported for beef cattle.

Heritability (h^2) can first be defined in the broad sense the degree to which individuals' phenotypes are determined by their genotypes (σ^2_G / σ^2_P, where σ^2_G and σ^2_P are the genotypic and phenotypic variances, respectively). A second definition, in the narrow sense, as an expression of the degree to which phenotypes are determined by the genes transmitted from the parents (σ^2_A / σ^2_P, where σ^2_A and σ^2_P are the additive genetic and phenotypic variances, respectively). Heritability in the broad sense or degree of genetic determination is of more theoretical interest while that in the narrow sense is of greater importance in breeding practice as it determines the degree of similarity between relatives. Therefore, heritability in the narrow sense will be the focus of the present discussion.

The heritability of a metric character is estimated using the methods of regression, correlation or analysis of (co) variances and concepts of the similarity between relatives. Heritability can be considered as the regression of an animals' breeding value on its phenotype and it can be expressed as :

$$\hat{h}^2 = \hat{b}_{A.P} = [\hat{\sigma}_{(A,P)}] / [\hat{\sigma}^2_P]$$

where :

$\hat{b}_{A.P}$ = estimated regression coefficient of the animal breeding value on phenotypic value,

$\hat{\sigma}_{(A,P)}$ = estimated covariance component between breeding and phenotypic value from relatives, and

$\hat{\sigma}^2_P$ = estimated phenotypic variance.

In practice, covariance between relatives are derived from its relationship to the additive genetic variance and the additive relationship. For instance, the additive

relationship between parent and offspring and between half-sib relatives are .5 and .25, respectively. Generally, the covariance between relative's records ($Cov_{i,j}$) is $a_{ij}\sigma^2_A$, where a is the additive relationship between relatives i and j. As a result,

$$\sigma^2_A = [1 / a_{ij}] [Cov_{i,j}].$$

By utilizing the concept of regression and coefficient of the additive variance in the covariance, heritability estimates can then be generally expressed as:

$$\widehat{h}^2 = [1 / a] [\widehat{\sigma}_{(A,P)}] / [\widehat{\sigma}^2_P],$$

where $\widehat{\sigma}_{(A,P)}$ is the covariance component estimate between breeding value and phenotypic value from relatives. In a case where the heritabilty is estimated from the paternal half-sib relative, the covariance between relatives is represented by the variance component between sires ($\widehat{\sigma}^2_S$) and environmental variance component is represented by the variance component within sires ($\widehat{\sigma}^2_W$) and the heritability is calculated as :

$$\widehat{h}^2 = 4 [\widehat{\sigma}^2_S] / [\widehat{\sigma}^2_S] + [\widehat{\sigma}^2_W].$$

The heritability can also be estimated by the regression of parents on the offspring. In a parent-offspring mean method, it can be expressed as :

$$\widehat{h}^2 = \widehat{b}_{OP} = [\widehat{\sigma}_{OP}] / [\widehat{\sigma}^2_X],$$

where $\widehat{b}_{OP}$, $\widehat{\sigma}_{OP}$ and $\widehat{\sigma}^2_X$ are the coefficient of regression of parents on offspring, covariance between parents and offspring and the phenotypic variance measured in offspring, respectively. The covariance which is computed from the cross-products of the paired values between parents and offspring, estimates .5 of the additive genetic variance. Therefore, the heritability can then be estimated by :

$$\widehat{h}^2 = 2 [\widehat{\sigma}_{OP}] / \widehat{\sigma}^2_X .$$

where $\widehat{\sigma}_{OP}$ is the estimated covariance between parent and offspring.

There are several designs for estimating the heritability by regression of offspring on parent. For instance, intra-sire regression of offspring on dam, regression of individual observations of progeny on dam's record for unequal progeny per dam and by weighting each family with the number of progeny used. In general, the heritability estimate by regression of offspring on parent is :

$$\widehat{h}^2 = [b / a]$$

where **b** is coefficient of regression and **a** is the additive relationship between parent and offspring. Several equations to calculate the heritability estimates are shown in table 2.2.

Based on its dimension, heritability can be classified as low (< .25), medium (.25 to .50) and high (> .50) (Preston and Willis, 1974).

2.4.1.2. Heritability estimates of some traits

Various studies have been carried out to examine heritability estimates of beef cattle production and reproduction traits. Production traits examined include birth weight, weaning weight, yearling weight, post-yearling weight and carcass traits. Heritabilities for reproduction traits such as scrotal circumference, sperm production, pubertal age, pubertal weight, pregnancy rate, gestation length, calving rate, calving difficulty, stillbirth, weaning rate and calving interval have been reported. Other traits that also influence the overall beef productivity are feed conversion rate, disease and parasite resistance. Results of these studies will be discussed in the next section.

2.4.1.2.1 *Birth weight*

Preston and Willis (1974) reviewed heritability estimates for birth weight of various breeds of beef cattle. The average value was .38 with a range from .00 to 1.00. Dealing with breeds of *Bos indicus*, Plasse (1978) summarized the heritability estimates of birth weight for breeds such as Brahman, Gir, Guzera and Nellore. The corresponding means (and ranges) for those breeds were .33 (.16 to .48), .57 (.26 to .89), .35 (.25 to .46) and .34 (.07 to .62), respectively. Recent paternal half-sib heritability estimates of birth weight of beef cattle breeds are given in table 2.3.

In summary, the heritability estimates of birth weight from the literature quoted are generally moderate to high.

Table 2.2. Equations for calculating heritability estimates based on regression, correlation and analysis of variance method [1].

Method	Formula
1. Regression parent on offspring	
1.1. One parent-offspring mean	$h^2 = 2\,[(\sigma_{PO})/\sigma^2_P\,]$
1.2. Mid-parent offspring mean	$h^2 = [(\sigma_{MPO})/\sigma^2_{MP}\,]$
2. Correlation coefficient	
2.1. Half-sib correlation	$h^2 = 4[\,(\sigma_{XY})\,/\sqrt{(\sigma^2_X)(\sigma^2_Y)}]$
2.2. Full sib correlation	$h^2 = 2[\,(\sigma_{XY})\,/\sqrt{(\sigma^2_X)(\sigma^2_Y)}]$
3. Analysis of variances	
3.1. Half-sib relationships	$h^2 = [4\,(\sigma^2_S)]\,/\,[\sigma^2_S + \sigma^2_W]$
3.2. Full-sib relationships	$h^2 = [2\,(\sigma^2_S)]\,/\,[\sigma^2_S + \sigma^2_W]$

[1] :
W : within sire
P : parent mean
PO : parent-offspring mean
MPO : mid-parent offspring mean
X : trait of X
Y : trait of Y
S : among sires

Table 2.3   Recent paternal half-sib heritability estimates of birth weight in beef cattle from various studies [1,2].

Breed	Sex	$h^2 \pm$ se	Authors
Bos indicus :			
Brazilian	C	.07 ± .11	Olson *et al.* (1984)
Gobra	C	.14	Abassa *et al.* (1989)
Gobra	C	.14 ± .06	Sow *et al.* (1988)
Sanga	C	.19 ± .06	Lubout and Swanapel (1990)
Getrudis	C	.24 ± .10	Aaron *et al.* (1987)
Brahman	C	.25 ± .13	Franke and Burns (1985)
Azanoak	M	.30	Chartier *et al.* (1983)
Getrudis	F	.32 ± .07	Aaron *et al.* (1987)
Brahman	C	.34 ± .04	Silva *et al.* (1988)
Gir	C	.35 + .09	Hoogestejn (1987)
Brahman cross	C	.38	Hetzel *et al.* (1990)
Getrudis	M	.38 ± .12	Aaron *et al.* (1987)
Azanoak	F	.41	Chartier *et al.* (1983)
Mashona	C	.44 ± .11	Tawonezvi (1989b)
Nellore	C	.46 ± .15	Tonhati *et al.* (1988)
Nellore	C	.62 ± .14	Olson *et al.* (1984)
Bos taurus :			
Hereford	M	.18 ± .04	DeNise *et al.* (1988)
Hereford	M	.19 ± .09	Trift *et al.* (1981)
Angus	C	.19	Wilson *et al.* (1986)
Hereford	F	.20 ± .04	DeNise *et al.* (1988)
Angus and Hereford	F	.27 ± .07	Smith *et al.* (1989b)
Angus and Hereford	M	.28 ± .08	Smith *et al.* (1989c)
Hereford	C	.35	Sharma *et al.* (1985)
Red Angus	M	.38 ± .06	Bourdon and Brinks (1982)
Hereford	F	.39 ± .12	Trift *et al.* (1981)

table 2.3 (Continued)

Hereford	C	.41	Wilson *et al.* (1986)
Angus	F	.41	Alenda and Martin (1987)
Red Angus	C	.46 ± .02	Winder *et al.* (1990)
Synthetic	C	.47	Sharma *et al.* (1985)
Angus	M	.51	Alenda and Martin (1987)
Hereford	M	.52	Itulya *et al.* (1987)
Angus	M	.70	Knights *et al.* (1984)

1 :

h^2 : heritability estimates
C : combination (males and females)
F : females
M : males
se : standard error

2 :

See reviews by Preston and Willis (1974) and Plasse (1978) for earlier h^2 estimates.

2.4.1.2.2 Weaning weight

Preston and Willis (1974) summarized estimates of weaning weight heritabilities of various breeds of beef cattle. The average value was .30 with a range from .00 to 1.00. Plasse (1978) summarized the heritability estimates of weaning weight for breeds such as Brahman in Latin America, Gir, Guzera and Nellore. The corresponding means (and ranges) for those breeds were .28 (.06 to .47), .48 (.36 to .60), .20 (.09 to .35) and .21 (.04 to .51), respectively. Recent paternal half-sib heritability estimates of weaning weight of beef cattle breeds are given in table 2.4.

In summary, the heritability estimates of weaning weight from the literature quoted are generally moderate to high.

2.4.1.2.3 Yearling weight

Dealing with breeds of *Bos indicus*, Plasse (1978) summarized the heritability estimates of yearling weight for breeds such as the Brahman (in Latin America), Gir, Guzera and Nellore. The average of the yearling weight heritability estimate for these breeds was .43 ranged from .12 to .67. Recent paternal half-sib heritability estimates for yearling weight of beef cattle breeds are given in table 2.5.

In summary, heritability estimates of yearling weight for beef cattle tend to be of moderate magnitude.

2.4.1.2.4 Post-yearling weight

Plasse (1978) summarized the heritability for post-yearling weight of *Bos indicus* ranged from .14 to .72 (an average of .53). Dalton (1980) in a summary of genetic parameters for beef cattle noted that heritability estimates for 18-month weight and final weight ranged from .30 to .55 and from .50 to .60, respectively. Recent heritability estimates for post-yearling body weight age are given in table 2.6.

In summary, it appears that heritability estimates for post-yearling weight in beef cattle are moderate to high.

Table 2.4   Recent paternal half-sib heritability estimates of weaning weight in beef cattle from various studies [1,2].

Breed	Sex	$h^2 \pm se$	Authors
Bos indicus :			
Sanga	C.	.05 ± .04	Lubout and Swanapel (1990)
Brazilian	C	.07 ± .11	Olson *et al.* (1984)
Gir	C	.09 + .04	Hoogestejn (1987)
Nellore	C	.12 ± .14	Olson *et al.* (1984)
Brahman	C	.12 ± .05	Olson *et al.* (1984)
Nellore	C	.13 ± .08	Bergman *et al.* (1984)
Nellore	C	.16	Oliveira and Duarte (1984)
Zebu	C	.18	Rico *et al.* (1982)
Brahman cross	C	.20	McKinnon *et al.* (1990)
Brahman	C	.26 ± .04	Silva *et al.* (1988)
Gobra	C	.28 ± .08	Sow *et al.* (1988)
Romosinuano	C	.29 ± .14	Tewolde (1988)
Nellore	C	.34 ± .06	Tonhati *et al.* (1988)
Brahman	C	.34 ± .09	Robinson (1990)
Gobra	C	.34	Abassa *et al.* (1990)
Brahman	C	.35 ± .15	Franke and Burns (1985)
Mashona	C	.38 ± .10	Tawonezvi (1989b)
Azanoak	M	.70	Chartier *et al.* (1982)
Azanoak	F	.84	Chartier *et al.* (1982)
Bos taurus :			
Charolais	C	.06	Laloe *et al.* (1988)
Charolais	C	.10 ± .09	Preisinger and Kalm (1988)
Hereford	M	.12 ± .12	Lamb *et al.* (1990)
Hereford	C	.13	Wilson *et al.* (1986)
Hereford	C	.13 ± .03	Pacho (1984)
Hereford	C	.14	Sharma *et al.* (1985)

table 2.4 (Continued)

Angus and Hereford	F	.14	Smith et al. (1989b)
Angus and Hereford	M	.10	Smith et al. (1989c)
Angus	C	.16	Wilson *et al.* (1986)
Hereford	M	.17 ± .11	Reynolds *et al.* (1989)
Angus	F	.21 ± .07	Alenda and Martin (1987)
Limousin	C	.23	Laloe *et al.* (1988)
Angus	M	.30 ± .08	Alenda and Martin (1987)
Red Angus	C	.39 ± .02	Winder *et al.* (1990)
Angus	M	.46 ± .05	Knights *et al.* (1984)
Red Angus and Hereford	M	.63 ± .08	Bourdon and Brinks (1982)

[1] : Abbreviations as for table 2.3 .

[2] : See reviews by Preston and Willis (1974) and Plasse (1978) for earlier h^2 estimates.

Table 2.5. Recent paternal half-sib heritability estimates of yearling weight in beef cattle from various studies [1,2].

Breed	Sex	$h^2 \pm$ se	Authors
Bos indicus :			
Sanga	C	.09 ± .45	Lubout and Swanepoel (1990)
Brahman	F	.13 ±.10	Pacho (1984)
Nellore	C	.14 ±.05	Olson *et al.* (1984)
Bunaji	C	.16 ±.27	Oni *et al.* (1989)
Zebu	C	.16 +.06	Planas (1987)
Nellore	C	.16 +.08	Bergman *et al.* (1984)
Brahman	M	.18 ±.16	Pacho (1984)
Nellore	C	.20 ±.03	Oliveira and Duarte (1984)
Brahman	C	.21 +.07	Robinson (1990)
Brahman Cross	C	.25	MacKinnon *et al.* (1990)
Nellore	C	.29 ±.06	Silva *et al.* (1988)
Gobra	C.	.33	Abassa *et al.* (1989)
Nellore	C	.36 ±.18	Pena *et al.* (1982)
Gobra	C	.41 ±.12	Sow *et al.* (1988)
Romosinuano	C	.57 ±.21	Tewolde (1988)
Azanoak	M	.65	Chartier *et al.* (1982)
Bos taurus :			
Hereford	F	.17	Itulya *et al.* (1987)
Angus	F	.18 +.0	Alenda and Martin (1987)
Hereford	M	.21 + .10	Itulya *et al.* (1987)
Hereford	C	.24	Sharma *et al.* (1985)
Charolais	C	.26 + .11	Preisinger and Kalm (1988)
Angus and Hereford	F	.29 ± .08	Smith *et al.* (1989b)
Angus and Hereford	M	.33 ± .09	Smith *et al.* (1989c)
Angus	M	.36 +.08	Alenda and Martin (1987)
Angus	M	.49 +.08	Knights *et al.* (1984)
Angus/ Hereford	F	.66 + .12	Bourdon and Brinks (1982)
Angus/ Hereford	M	.73 +.11	Bourdon and Brinks (1982)

[1] : Abbreviations as for table 2.3 .
[2] : See review by Plasse (1978) for earlier h^2 estimates.

Table 2.6 **Recent paternal half-sib heritability estimates for beef cattle post-yearling weight from various studies** [1,2,3].

Breed	Sex	$h^2 \pm se$	Age	Authors
Bos indicus :				
Nellore	C	.12	550 d	Oliveira and Duarte (1984)
Nellore	C	.13 + .05	18 mo	Olson *et al.* (1984)
Sanga	C	.14 ± .06	540 d	Lubout and Swanepoel (1990)
Gobra	C	.15	18 mo	Abassa *et al.* (1990))
Gobra	C	.16 ± .12	36 mo	Sow *et al.* (1988)
Nellore	C	.18 + .06	24 mo	Olson *et al.* (1984)
Brahman	C	.18	18 mo	Ordonez *et al.* (1984)
Brahman cross	C	.19	18 mo	Boada (1977)
Brahman cross	C	.20 ± .07	700 d	Robinson (1990)
Gobra	C	.21 ± .13	24 mo	Sow *et al.* (1988)
Brahman	F	.22	18 mo	Olson *et al.* (1984)
Brahman	M	.25	18 mo	Olson *et al.* (1984)
Gobra	C	.27 ± .14	18 mo	Sow *et al.* (1988)
Brahman cross	C	.31 ± .08	18 mo	Robinson (1990)
Brahman cross	C	.32 ± .09	900 d	Robinson (1990)
Bos taurus :				
Simmental	C	.26	18 mo	MacKinnon *et al.* (1990)
Various	M	.29 ± .09	20 mo	Morris *et al.* (1990)
Hereford	F	.31	20 mo	Itulya *et al.* (1987)
Hereford	M	.34 ± .09	19 mo	Sivarajasingam *et al.* (1988)
Hereford	F	.35	24 mo	Itulya *et al.* (1987)
Hereford	F	.35 ± .12	20 mo	DeNise and Torabi (1989)
Hereford	M	.41 ± .15	24 mo	Itulya *et al.* (1987)
Hereford	M	.46 ± .15	20 mo	Itulya *et al.* (1987)
Hereford	M	.55 ± .22	20 mo	DeNise and Torabi (1989)
Angus cross	C	.69 ± .20	18 mo	Johnson *et al.* (1986)
Various	M	.56 ± .19	31 mo	Morris *et al.* (1990)

[1] : mo and d are month and day of age, respectivly.
[2] : Other abbreviations as for table 2.3 .
[3] : See reviews by Plasse (1978) and Dalton (1980) for earlier h^2 estimates.

2.4.1.2.5 Carcass traits

Preston and Willis (1974) in a summary of heritability estimates for beef carcass traits noted that the values for traits such as carcass weight, dressing percentage and fat thickness ranged from .20 to .49, .10 to .74, .24 to .74, respectively. Dalton (1980) noted heritability estimates for carcass traits such as carcass grade (ranged from .35 to .45), rib eye area (.70) and fat thickness (0.45). Koch et al., (1982) reported averages of heritability estimates for carcass traits such as carcass weight (.55), fat thickness(.48), rib eye area (.40) and marbling of beef cattle (.42). Recent heritability estimates for carcass traits are given in table 2.7.

In summary, the heritability estimates of carcass traits such as carcass weight, bone weight, fat thickness and rib eye are moderate to high.

2.4.1.2.6 Reproductive traits

Scrotal circumference is the useful indicator of fertility in bulls as it is highly correlated with total sperm production (Hanh et al., 1969), related to semen quality (Brinks et al., 1978), an indicator of puberty in bulls (Lunstra, 1978), indicates age at puberty and fertility in female offspring (Brinks et al., 1978 and Smith et al., 1989a) and it is highly correlated with the pregnancy rate of females (Coulter et al., 1979 and Toelle and Robison, 1985). Coulter et al. (1976) noted an average value of .67 ± .10 for scrotal circumference heritability estimates based on 389 observations in Holstein bulls with age from 6 to 71 months. More recent heritability estimates of scrotal circumference are given in table 2.8.

Preston and Willis (1974) in a summary of heritability estimates of female reproductive traits for various beef cattle breeds noted average values for gestation length (.40), calving interval(.08), conception rate (.08), age at first oestrus (.38) and percentage of calf survival (.05). Dalton (1980) reported ranges of heritability estimates for reproductive traits such as number of calves born (0 to .15), number of calves weaned (0 to .10) and calving interval (0 to .15). Thorpe and Cruickshank (1981) found the heritability estimate for calving percentage based on the dam-daughter regression for various breeds of Bos indicus ranged from 0.08 to .38 with an average of .20. Recent paternal half-sib heritability estimates of female reproductive traits are shown in table 2.8.

Table 2.7. Recent paternal half-sib heritability estimates for carcass traits from various studies on beef cattle [1,2].

Traits	Age	Breed	Sex	$h^2 \pm se$	Authors
Carcass weight :					
	-	Charolais	M	.20 ± .10	Renand and Gaillard (1982)
	20 mo	Various	M	.28 ± .09	Morris *et al.* (1990)
	31 mo	Various	M	.44 ± .18	Morris *et al.* (1990)
	yearling	Hereford	M	.31 ± .15	Lamb *et al.* (1990)
	21-24 mo	Friesian	M	.32 ± .23	More O'ferall *et al.* (1989)
	yearling	Various	M	.36 ± .09	McNeil *et al.* (1984)
	-	Hereford	M	.38 ± .18	Reynolds *et al.* (1987)
	-	Hereford	M	.48 ± .04	Benyshek (1981)
	yearling	Various	M	.58	Koch *et al.* (1982)
	452 d	Hereford	F	.68 ± .25	Koch (1978)
Dressing percentage :					
	20 mo	Various	M	.14 ± .07	Morris *et al.* (1990)
	-	Hereford	M	.25 ± .17	Reynolds *et al.* (1987)
	-	Hereford	M	.31 ± .04	Benyshek (1981)
	31 mo	Various	M	.39 ± .18	Morris *et al.* (1990)
	yearling	Various	M	.63	Koch *et al.* (1982)
	-	Charolais	M	.68 ± .10	Renand and Gaillard (1982)
Fat depth (mm) :					
	20 mo	Various	M	.30 ± .14	Morris *et al.* (1990)
	31 mo	Various	M	.37 ± .18	Morris *et al.* (1990)
	yearling	various	M	.41	Koch *et al.* (1982)
	-	Hereford	M	.49 ± .04	Benyshek (1981)
	452 d	Hereford	F	.68 ± .25	Koch (1978)
Rib eye area :					
	yearling	Hereford	M	.28 ± .15	Lamb *et al.* (1990)
	452 d	Hereford	F	.28 ± .24	Koch (1978)
	-	Hereford	M	.40 ± .04	Benyshek (1981)
	yearling	Various	M	.56	Koch *et al.* (1982)
Marbling :					
	yearling	Hereford	M	.33 ± .15	Lamb *et al.* (1990)
	452 d	Hereford	F	.34 ± .25	Koch (1978)
	yearling	Various	M	.40	Koch *et al.* (1982)

[1] : Abbreviations as for table 2.3 and 2.6 .
[2] : See review by Preston and Willis (1974), Dalton (1980) and Koch *et al.* (1982) for earlier h^2 estimates.

Table 2.8   Recent paternal half-sib heritability estimates for reproductive trait from various studies on beef cattle [1,2].

Traits	Breed	Age (day)	h² ± se	Authors
Male				
Scrotal circumference :				
	Angus	365	.38 ± .16	Latimer *et al.* (1982)
	Hereford, Angus	365	.44 ± .24	Neely *et al.* (1982)
	Hereford	365	.49 ± .06	Bourdon and Brinks (1986)
	Various	730	.54	Coulter *et al.* (1987)
	Angus	205	.60 ± .17	Latimer *et al.* (1982)
	Hereford	600	.60 ± .09	Sivarajasingam *et al.* (1990)
	Various	365	.69	Coulter *et al.* (1987)
Fertility :				
	African cross		.08	MacKinnon *et al.* (1990)
	Brahman		.08	MacKinnon *et al.* (1990)
	Various		.08	MacKinnon *et al.* (1990)
	Brahman cross		.10	MacKinnon *et al.* (1990)
	Africander		.12	MacKinnon *et al.* (1990)
	Danish		.03	Hansen (1979)
Female				
Age at puberty :				
	Hereford		.10 ± .17	Smith *et al.* (1989b)
	Various		.31 ± .19	Morris *et al.* (1986)
	Various		.61 ± .17	MacNeil *et al.* (1984)
Weight at puberty :				
	Various		.45 ± .19	Morris *et al.* (1986)
	Various		.70 ± .11	MacNeil *et al.* (1984)
Pregnancy rate :				
	Hereford		.03 ± .00	Budenberg *et al.* (1989)
	Polish		.04 ± .02	Brzozowski (1987a)
	Angus		.19 ± .01	Budenberg *et al.* (1989)
	Africander		.06	MacKinnon *et al.* (1990)
	Brahman cross		.07	MacKinnon *et al.* (1990)
	African cross		.12	MacKinnon *et al.* (1990)
	Brahman		.13	MacKinnon *et al.* (1990)
	Brahman		.25 ± .17	Cruz *et al.* (1978)

Continued table 2.8 (continued)

Gestation length :

	Polish	.16 ± .02	Brzozowski (1987b)
	Simmental	.24	Kemp *et al.* (1988)
	Brown swiss	.41	Hagger and Hofer (1990)
	Braunvieh	.45	Hagger and Hofer (1990)
	Simmental	.50	Hagger and Hofer (1990)
	Charolais	.67 ± .26	Duarte *et al.* (1986)

Calving difficulty :

	Red Polish	.02	Zarnecki (1982)
	Black Polish	.06	Zarnecki (1982)
	Brauvieh	.08	Hagger and Hofer (1990)
	Brown Swiss	.09	Hagger and Hofer (1990)
	Simmental	.11	Hagger and Hofer (1990)
	Charolais	.21 ± .17	Duarte *et al.* (1986)
	Various	.22 ± .18	MacNeil *et al.* (1984)

Live calf :

	Brahman (one week)	.11 ± .12	Cruz *et al.* (1978)
	Brahman (at birth)	.15 ± .03	Cruz *et al.* (1978)
	Hereford (at birth)	.64 ± .21	Milagres *et al.* (1979)

Stillbirth :

	Brauvieh	-.02	Hagger and Hofer (1990)
	Brown Swiss	.01	Hagger and Hofer (1990)
	Simmental	.015	Hagger and Hofer (1990)

Calving rate :

	Hereford	.01 ± .02	Milagres *et al.* (1979)
	Brahman	.14	Deese and Koger (1967)
	Brahman cross	.31	Deese and Koger (1967)
	Zebu cross	.44	Turner (1982)

Calving interval :

	Polish	.03 ± .02	Brzozowski (1987a)
	Simmental	.04 ± .05	Meacham and Notter (1987)
	Zebu cross	.04	Alencar *et al.* (1987)
	Chanchin	.05	Alencar *et al.* (1987)
	Red Danish	.09	Hansen (1979)

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[1] : Abbreviations as for table 2.3 .

[2] : See reviews by Preston and Willis (1974), Coulte *et al.* (1976) and Plasse (1978) for earlier h^2 estimates for the scrotal circumference and female reproductive performance.

In summary, scrotal circumference is moderately to highly heritable while other reproductive traits are lowly to moderately heritable. The heritability for fertility in subtropical and tropical environments looks to be moderate which is higher than in temperate environments.

2.4.1.2.7 Other traits

Another important trait for to the overall beef production system is the efficiency of feed utilization which can be defined as the ratio of average daily feed intake to average daily gain. It is of central importance as it reflects aspects such as high daily gain relative to mean weight, leaner gain and lower maintenance requirement per kg of metabolic weight (Hanset *et al.*, 1987). Preston and Willis (1974) and Thiessen *et al.* (1985) in their summaries of heritability estimates for feed conversion ratio noted average values of .40 and .45, respectively. Recent heritability estimates of feed utilization are given in table 2.9. In general, heritability estimates of feed utilization in beef cattle tend to be moderate to high.

Disease and parasite resistance also deserve consideration in beef breeding programs. If resistance is heritable, there is the possibility to develop strains of cattle with genetic resistance to parasites and / or diseases. Hewetson (1968) observed a zero heritability estimate for tick resistance at the first infestion on Zebu steers. However, the fourth and fifth infestions heritability estimates were .28 and .42, respectively. Emanuelson (1988) summarized estimates of mastitis and ketosis in dairy cattle finding averages of .09 and .04, respectively. Other heritability estimates of disease and parasite resistance of beef cattle are given in table 2.10. In general, results indicate that there is a low heritability for diseases such as mastitis, ketosis and nematode resistance and a moderate to high heritability for tick resistance in cattle.

2.4.2. Correlation

2.4.2.1. Introduction

Correlations, either phenotypic (the association between characters which can be observed directly) or genetic correlations (the association between breeding values), are important parameters from the practical genetic improvement point of

Table 2.9   Recent paternal half-sib heritability estimates for feed efficiency from various studies on beef cattle [1,2].

Breed	Sex	$h^2 \pm se$	Authors
Hereford	M	.13 ± .08	Brown *et al.* (1988)
Angus	M	.14 ± .07	Brown *et al.* 1988)
Danish	M	.36 ± .07	Andersen (1978)
Belgian	M	.39	Hanset *et al.* (1987)
Hereford, Angus	M	.46 ± .21	Neely *et al.* (1982)
Norwegian Red	M	.59 ± .26	Fimland (1973)
Various	M	.86	Khalil and Pirchner (1986)

[1]   :   Abbreviations as for table 2.3 .

[2]   :   See review by Preston and Willis (1974) and Thiessen *et al.* (1985) for other h^2 estimates.

Table 2.10. Recent heritability estimates for disease and parasite resistance from various studies on beef cattle [1,2,3].

Breed	Sex	Characters	$h^2 \pm se$	Method	Authors	Comment
Bos indicus :						
Zebu cross	M	Tick resistence	.00	phs	Hewetson (1968)	First infestation
Zebu cross	M	Tick resistence	.28	phs	Hewetson (1968)	Fouth infestation
Zebu cross	M	Tick resistence	.42	phs	Hewetson (1968)	Fifth infestation
Bos taurus :						
Various	C	Nematode resistence	.04	phs	Barlow and Piper (1985)	Faecal egg counts and larva differentiation
Shorthorn	F	Tick resistance	.39	dcc	Wharton *et al.* (1970)	
Angus	C	Helminth resistence	.40 ±.15	phs	Leighton *et al.* (1988)	Eggs per gram of feces.
Shorthorn	F	Tick resistance	.49	Fsc	Wharton *et al.* (1970)	
Angus	C	Helminth resistence	.78	phs	Seifert (1977)	total species

1 : phs, dcc and fsc are paternal halb-sib, daughter-cow correlation and full-sib correlation, respectively.
2 : Other abbreviations as for table 2.3 .
3 : See Heweston (1968) and a review by Emanuelson (1988) for other h^2 estimates.

view. The sign and size of correlations will be determined by the magnitude of covariance components between two traits and variance components of each trait. Together with other parameters such as phenotypic, genetic variance and covariance, and the economic value, they are needed to derive selection index weights. A genetically correlated indicator trait can be used to improve economic traits that are difficult or expensive to be measured. For instance, selection for growth traits may increase the feed efficiency ration and selection for carcass weight can only be based on yearling weight. Genetic correlations are also important to be considered if there are antagonistic correlations between traits to avoid inappropriate selection as selection to increase one character may decrease another. It is necessary to understand concepts such as the apportioning of phenotypic covariance into environmental and genetic covariance and the methodology for calculating the correlation between two traits before reviewing estimates that have been reported for beef cattle.

With the assumption that there is no interaction between genetic and environmental effects, the phenotypic covariance is able to be apportioned into the genetic and environmental covariances. Generally, the genetic covariance is the sum of the additive, dominant and epistatic covariance. However, from the practical point of view the additive genetic effect is the most important component. Therefore, the phenotypic covariance is simply the sum of the additive genetic covariance and the environmental covariance components, assuming the absence of dominant and epistatic effects.

Factors such as pleiotropy and linkage are the important causes for genetic correlation between traits. Pleiotropy is the process where one gene may affect two or more traits and linkage is where genes occur nearby each other on the same chromosome and tend to be passed as a package. Some genes may affect 2 traits in the same direction, while others may affect the 2 traits in opposite directions. The first case will cause a positive genetic correlation while the second case leads to a negative genetic relationship between traits.

Correlations between two traits can be estimated by utilizing the concepts of the additive correlation among relatives. Variance and covariance component estimates are derived from the various statistical model analyses of characters measured on an individual and its relatives. They can be calculated by the general formula :

$$\hat{r}_{X1X2} = [\hat{\sigma}_{X1,X2}] / [(\hat{\sigma}_{X1})(\hat{\sigma}_{X2})]$$

where :

$\hat{r}$ = estimated correlation

$\acute{X}$ = can be either P (phenotypic) or A (additive genetic),

1, 2   = character 1 and 2, respectively,

$\hat{\sigma}_{X1,X2}$ = estimated covariance between X1 and X2,

$\hat{\sigma}_{X1}$ = estimated standard deviation of X1, and

$\hat{\sigma}_{X2}$ = estimated standard deviation of X2.

Genetic correlation coefficients can also be estimated through utilizing the concept of the cross-covariance between parent-offspring and additive genetic covariance between relatives (Falconer, 1981). The cross-covariance between parent and offspring estimates .5 the genetic covariance between characters. By regarding that additive relationship between parent and offspring is .5, the genetic correlation can then be estimated by:

$$\hat{r}_A = [\hat{\sigma}_{1,2}] / \sqrt{[(\hat{\sigma}_{1,1})(\hat{\sigma}_{2,2})]}$$

where:

$\hat{r}_A$ = estimated genetic correlation of between characters,

$\hat{\sigma}_{1,2}$ = estimated cross-covariances of offspring and parents for value of character 1 in parent and value of character 2 in offspring,

$\hat{\sigma}_{1,1}$ = estimated offspring-parent covariance for the character 1, and

$\hat{\sigma}_{2,2}$ = estimated offspring-parent covariance for the character 2.

Correlation estimates are broadly classified as negligible (- 0.1 to 0.1), low (- 0.3 to - 0.2 and 0.2 to 0.3), medium (- 0.5 to - 0.4 and 0.4 to 0.5) and high (-1.0 to - 0.6 and 0.6 to 1.0) (Dalton, 1980).

The next sections discuss both phenotypic and genetic correlation amongst various traits such as body weights (birth, weaning, yearling and post-yearling), body weight and carcass traits (carcass weight, killing out percentage and fat depth) and between body weight and reproductive performance (scrotal measurement, pregnancy rates, sperm production, age at puberty, gestation length, age at first calving, calving difficulties, calving rate, stillbirth and calf survival). Scrotal circumference is of central importance of male reproductive performance as it is a good indicator of sexual behaviour, age at puberty of related females, female reproductive performance, milk and fat production of daughters.

2.4.2.2. Estimates of phenotypic correlation

2.4.2.2.1 *Birth weight and weaning, yearling and post-yearling weight*

Preston and Willis (1974) summarized the phenotypic correlation between birth weight and weaning weight of beef cattle. The average value was .38 with a range from .30 to .42. Recent phenotypic correlation estimates between birth weight and weaning weight for beef cattle breeds are given in table 2.11.

Woldehawariat *et al.*, 1977 (cited by Thrift *et al.*, 1981) summarized the phenotypic correlation between birth weight and yearling weight of beef cattle and noted an average value of .43. Recent phenotypic correlation estimates between birth weight and yearling weight for beef cattle breeds are given in table 2.11.

Trail *et al.* (1971) observed an average value of .35 for the phenotypic correlation between the birth weight trait and the body weight at age of 15-, 18-, 21- and 24 month for crossbred beef cattle. Recent phenotypic correlation estimates between birth weight and yearling weight for beef cattle breeds are given in table 2.11.

In summary, the estimates of the phenotypic correlation between birth weight and other body weight such as weaning, yearling and post-yearling weight in beef cattle are moderate positive.

Table 2.11   Recent phenotypic correlation estimates between birth weight and weaning, yearling and post-yearling weight from various studies on beef cattle [1,2].

Traits	Breed	Sex	$r_p \pm se$	Authors
Weaning weight				
	Mashona	C	.18	Tawonezvi (1989b)
	Getrudis	F	.27	Aaron *et al.* (1987)
	Sanga	C	.27	Lubout and Swanepoel (1990)
	Getrudis	C	.29	Aaron *et al.* (1987)
	Romosinuano	C	.30	Tewolde (1988)
	Gobra	C	.31	Sow *et al.* (1988)
	Getrudis	M	.31	Aaron *et al.* (1987)
	Hereford	M	.33	Thrift *et al.* (1981)
	Angus	M	.34	Alenda and Martin (1987)
	Angus	M	.35	Knights *et al.* (1984)
	Hereford	F	.36	Thrift *et al.* (1981)
	Angus	C	.38	Winder *et al.* (1990)
	Angus	F	.40	Alenda and Martin (1987)
	Brahman	C	.48	Franke and Burn (1985)
Yearling weight				
	Romosinuano	C	.21	Tewolde (1988)
	Sanga	C	.25	Lubout and Swanepoel (1990)
	Hereford	M	.32	Thrift *et al.* (1981)
	Angus	F	.35	Alenda and Martin (1987)
	Angus	M	.37	Alenda and Martin (1987)
	Hereford	F	.39	Thrift *et al* (1981)
	Angus	C	.39	Winder *et al.* (1990)
	Angus	M	.43	Knights *et al.* (1984)
Post-yearling weight				
	Mashona	C	.16	Tawonezvi (1989b)
	Sanga	C	.16	Lubout and Swanepoel (1990)
	Romosinuano (18 mo)	C	.17	Tewolde (1988)
	Romosinuano (24 mo)	C	.22	Tewolde (1988)

[1]   :   Abbreviations as for table 2.3 and table 2.6 .

[2]   :   See Trail (1971) and reviews by Preston and Willis (1974) and Plasse (1978) for earlier r_p estimates.

2.4.2.2.2 Weaning weight and yearling and post-yearling weight

Woldehawariat, 1977 (cited by Thrift *et al.*, 1981) summarized phenotypic correlation between weaning and yearling weight for beef cattle breeds. They found the average value of .70. Recent phenotypic correlation estimates between weaning and yearling weight of beef cattle breeds are given in table 2.12.

Preston and Willis (1974) reviewed phenotypic correlations between weaning weight and final weights of performance tests in beef cattle. They reported an average value of .51 with a range from .16 to .72. An average of .65 with a range from .53 to .87 for the phenotypic correlation between weaning and post-yearling weight was summarized by Plasse (1978) in *Bos indicus* beef breeds. Recent paternal half-sib phenotypic correlation estimates between weaning and post-yearling weight of beef cattle breeds are given in table 2.13.

In summary, reported estimates of the phenotypic correlation between weaning weight and yearling and post-yearling weight in beef cattle are moderate to highly positive.

2.4.2.2.3 Yearling and post-yearling weight

Trail *et al.* (1971) reported value of .87, .90, .86 and .79 for the phenotypic correlation between yearling weight and weight at 15-, 18-, 21-, and 24-month, of age, respectively, in several *Bos indicus* crossbreds. Plasse and Verde (1976) (cited by Plasse, 1978) reported phenotypic correlations between yearling weight and 16-month weight (.70) and with 24-month weight (.38). More recent phenotypic correlation estimates between yearling and post-yearling weight of beef cattle breeds are given in table 2.14.

In summary, the estimates of the phenotypic correlation between yearling weight and post-yearling weight in beef cattle are moderate to highly positive.

Table 2.12   **Recent phenotypic correlation estimates between weaning and yearling weight from various studies on beef cattle [1,2].**

Breed	Sex	$r_p \pm se$	Authors
Bos indicus			
Bunaji	C	.48	Oni *et al.* (1989)
Sanga	C	.73	Lubout and Swanepoel (1990)
Romosinuano	C	.74	Tewolde (1988)
Gobra	C	.76	Sow *et al.* (1988)
Bos taurus			
Angus	M	.35	Knights *et al.* (1984)
Red Angus	C	.63	Winder *et al.* (1990)
Hereford	C	.70	Itulya *et al.* (1987)
Angus	F	.71	Alenda and Martin (1987)
Angus and Hereford	M	.76	Bourdon and Brinks (1982)
Angus and Hereford	F	.76	Bourdon and Brinks (1982)
Angus	M	.77	Alenda and Martin (1987)

[1]   :   Abbreviations as for table 2.3 .

[2]   :   See a review by Woldehawariat *et al.* (1977) (cited by Trift *et al.*, 1981) for earlier r_p estimates.

Table 2.13 **Recent phenotypic correlation estimates between weaning weight and post-yearling weight from various studies on beef cattle [1,2].**

Breed	Age at post-yearling	$r_p \pm se$	Authors
Bos indicus :			
Gobra	36 mo	.43	Sow *et al.* (1988)
Sanga	540 d	.51	Lubout and Swanepoel (1990)
Gobra	24 mo	.57	Sow *et al.* (1988)
Mashona	18 mo	.69	Tawonezwi (1989b)
Gobra	18 mo	.73	Sow *et al.* (1988)
Bos taurus :			
Hereford	20 mo	.58	DeNise and Torabi (1989)
Hereford	24 mo	.61	Itulya *et al.* (1987)
Hereford	20 mo	.62	Itulya *et al.* (1987)
Angus cross	20 mo	.66	Johnson *et al.* (1986)

[1]   :   Abbreviations as for table 2.3 and 2.6 .

[2]   :   See reviews by Preston and Willis (1974) and Plasse (1978) for earlier r_p estimates.

Table 2.14 **Recent phenotypic correlation estimates between yearling weight and post-yearling weight from various studies on beef cattle** [1,2].

Breed	Age at post-yearling	Sex	$r_p \pm$ se	Authors
Gobra	36 mo	C	.51	Sow *et al.* (1988)
Sanga	540 d	C	.58	Lubout and Swanepoel 1990
Hereford	20 mo	F	.62	Itulya *et al.* (1987)
Gobra	24 mo	C	.69	Sow *et al.* (1988)
Hereford	24 mo	F	.72	Itulya *et al.* (1987)
Hereford	24 mo	F	.73	DeNise and Ray 1987
Gobra	18 mo	C	.76	Abassa *et al.* (1990)
Gobra	18 mo	C	.78	Sow *et al.* (1988)
Hereford	20 mo	F	.78	DeNise and Ray (1987)
Angus cross	20 mo	M	.82	Johnson *et al.* (1986)

[1]   :   Abbreviations as for table 2.3 and 2.6 .

[2]   :   See Trail *et al.* (1971) and Plasse and Verde (1976) for earlier r_p estimates.

2.4.2.2.4 Body weight and carcass traits

Preston and Willis (1974) summarized the phenotypic correlation between weaning weight and carcass traits such as carcass grade (average = .14) and fat thickness (average = -.26). Recent phenotypic correlation estimates between body weight and carcass trait of beef cattle breeds are given in table 2.15.

In summary, estimates of the phenotypic correlations between body weights and carcass traits such carcass weight, dressing percentage, fat depth and rib eye area of beef cattle are moderate to highly positive.

2.4.2.2.5 Body weights and reproductive traits

Coulter and Foote (1977) found a phenotypic correlation of .51 between body weight of bulls at 12 to 17 month of age and scrotal circumference for Holstein bulls. Lustra *et al.* (1978) reported an average value of phenotypic correlation of .80 between body weights (age at 7 to 13 months) and scrotal circumference for six breeds of cattle. Recent phenotypic correlation between body weight traits and scrotal circumference for beef cattle breeds are shown in table 2.16.

Phillipson (1976) reported that the phenotypic correlation between birth weight and gestation length, stillbirth and calving difficulties in Swedish cattle breeds were .28 (average of two values), .08 (average of two values) and .24 (average of six values ranged from .19 to .31), respectively. Burferning *et al.* (1978) found phenotypic correlations between birth weight and calving ease score (from 1 for no assistance to 4 for caesarian section) and gestation length for Simmental cattle were .31 and .20, respectively and between weaning weight and calving ease score and gestation length were .03 and .04, respectively. Morris (1980) reviewed the phenotypic correlations of live weights with heifer traits at or near puberty. The average phenotypic correlation between weaning weight and age at puberty and weight at puberty were -.29 (a range from -.17 to .41) and .46 (a range from .22 to .61). Recent phenotypic correlation estimates between body weight traits and female reproductive traits are shown in table 2.16.

Table 2.15   Recent phenotypic correlation estimates between body weight and carcass traits from various studies on beef cattle [1,2].

Carcass Trait (at age)	Body weight at			Breed	Authors
	Weaning	Yearling	Post-yearling (age)		
Carcass weight :					
434 d	.57	.95	-	Hereford	Shelby *et al.* (1963)
452 d	.59	.94	-	Hereford	Koch (1978)
20 mo	-	-	.91 (20 mo)	various	Morris *et al.* (1990)
31 mo	-	-	.92 (31 mo)	various	Morris *et al.* (1990)
	-	.96	-	Hereford	Lamb *et al.* (1990)
20 mo	.64	.81	.95 (2o mo)	Angus cross	Johnson *et al.* (1986)
Dressing % :					
434 d	.18	.19	-	Hereford	Shelby *et al.* (1963)
20 mo	.07	.17	.17 (2o mo)	Angus cross	Johnson *et al.* (1986)
Fat depth :					
452 d	.12	.33	-	Hereford	Koch (1978)
20 mo	.13	.12	.15 (20 mo)	Angus cross	Johnson *et al.* (1986)
20 mo	-	-	.15 (20 mo)	Various	Morris *et al.* (1990)
31 mo	-	-	.11 (31 mo)	Various	Morris *et al.* (1990)
Rib eye area :					
452 d	.23	.35	-	Hereford	Koch (1978)
	.21	.28	.34 (20 mo)	Angus cross	Johnson *et al.* (1986)
434 d	.24	.41	-	Hereford	Shelby *et al.* (1963)
	-	.51	-	Hereford	Lamb *et al.* (1990)

[1]   :   Abbreviations as for table 2.3 and 2.6 .

[2]   :   See a review by Preston and Willis (1974) for earlier r_p estimates.

Table 2.16 Recent phenotypic correlation estimates between body weights and reproductive traits from various studies on beef cattle [1,2].

Reproductive Traits	Body weight at				Breed	Authors
	Birth	Weaning	Yearling	Post-yearling		
MALE :						
Scrotal circumference :						
(205 d)	-	.57	.54	-	Hereford	Neely *et al.* (1982)
(365 d)	.15	.19	.26	-	Angus	Knights *et al.* (1984)
(365 d)	.11	.28	.37	-	Hereford	Bourdon and Brinks (1986)
(365 d)	-	.33	.43	-	Hereford and Angus	Smith *et al.* (1989c)
(365 d)	-	.43	.50	-	Hereford	Neely *et al.* (1982)
(600 d)	-	-	-	.35	Hereford	Sivarajasingam *et al.* (1988)
Sperm production :						
	.04	.08	.08	-	Angus	Knights *et al.* (1984)
	-	.22	.24	-	Hereford	Neely *et al.* (1982)
Percent normal sperm						
	-	-.04	.11	-	Hereford and Angus	Smith *et al.* (1989c)

table 2.16 (continued)

FEMALE :

Age at puberty :

-	-.17	-.16	-	Hereford and Angus	Smith *et al.* (1989b)

Gestation length

.27	-	-	-	Black and White Swiss	Hagger and Hofer (1990)
.30	-	-	-	Braunvieh	Hagger and Hofer (1990)
.30	-	-	-	Simmental	Hagger and Hofer (1990)
.43	-	-	-	Various	Cundiff *et al.* (1986)

Age at first calving :

-	.32	.27	-	Hereford	Smith *et al.* (1989b)
-	-.0	-.02	-	Hereford, Angus	Bourdon and Brinks (1982)

Calving difficulty :

.21	-	-	-	Braunvieh	Hagger and Hofer (1990)
.29	-	-	-	Various *Bos taurus* breeds	Cundiff *et al.* (1986)
.30		-	-	Black and White Swiss	Hagger and Hofer (1990)
.34	-	-	-	Simmental	Hagger and Hofer (1990)

Calf survival

-.07	-	-	-	Various	Cundiff *et al.* (1986)

Stillbirth

-.01	-	-	-	Braunvieh	Hagger and Hofer (1990)
.06	-	-	-	Black and White Swiss	Hagger and Hofer (1990)
.09	-	-	-	Simental	Hagger and Hofer (1990)

---

[1] : Abbreviations as for table 2.6 .

[2] : See reviews by Coulter and Foote (1977) and Lustra *et al.* (1978) for earlier r_p estimates between body weight and scrotal circumference and Phillipson (1976) and Burfening *et al.* (1978) for birth weight and female reproductive traits.

In summary, estimated phenotypic correlations between scrotal circumference and body weights in cattle are moderate to high. There is a moderate positive phenotypic correlation between birth weight and calving difficulties, a moderate negative for that between weights and age at puberty and a moderate to highly positive for that between weaning weight and weight at puberty. In general, the phenotypic correlations between body weights and the number of stillbirths are low.

2.4.2.3. Estimates of genetic correlation

2.4.2.3.1 Birth weight and weaning, yearling and post-yearling weight

Preston and Willis (1974) summarized genetic correlations between birth weight and weaning weight of beef cattle. They found an average value of .69 with a range from .21 to 1.12. Recent genetic correlation estimates between birth weight and weaning weight of beef cattle are given in table 2.17.

Woldehawariat *et al.*, 1977 (cited by Thrift *et al.*, 1981) summarized genetic correlations between birth weight and yearling weight of beef cattle. They reported an average value of .60. Recent genetic correlation estimates between birth weight and yearling of beef cattle are given in table 2.17.

Trail *et al.* (1971) reported an average value of .75 with a range from .58 to .81 of genetic correlations between birth weight and some post-yearling weights in *Bos indicus* crosses. Recent genetic correlation estimates between birth weight and some post-yearling weights of beef cattle are given in table 2.17.

In summary, the estimates of the genetic correlation between birth weight and other body weights such as weaning, yearling and some post-yearling weights in beef cattle are moderate to highly positive.

Table 2.17   Recent paternal half-sib genetic correlation estimates between birth weight and weaning, yearling and post-yearling weight from various studies on beef cattle [1,2].

Traits	Breed	Sex	$r_g \pm se$	Authors
Weaning weight				
	Hereford	M	.05 ± .37	Thrift *et al.* (1981)
	Brahman	C	.11 ± .38	Franke and Burns (1985)
	Sanga	C	.25	Lubout and Swanepoel (1990)
	Getrudis	F	.33 ± .22	Aaron *et al.* (1987)
	Angus	F	.36 ± .10	Alenda and Martin (1987)
	Hereford	F	.36 ± .37	Thrift *et al.* (1981)
	Getrudis	C	.40 ± .14	Aaron *et al.* (1987)
	Mashona	C	.42 ± .18	Tawonezvi (1989b)
	Getrudis	M	.43 ± .21	Aaron *et al.* (1987)
	Angus	M	.57 ± .10	Alenda and Martin (1987)
	Angus	C	.56	Winder *et al.* (1990)
	Angus	M	.59	Knights *et al.* (1984)
	Romosinuano	C	.67 ± .24	Tewolde (1988)
Yearling weight				
	Hereford	M	.20 ± .30	Thrift *et al.* (1981)
	Hereford	F	.44 ± .43	Thrift *et al.* (1981)
	Romosinuano	C	.48 ± .26	Tewolde (1988)
	Angus	M	.77 ± .11	Alenda and Martin (1987)
	Angus	F	.45 ± .09	Alenda and Martin (1987)
	Angus	M	.57	Knights *et al.* (1984)
	Sanga	C	.11	Lubout and Swanepoel (1990)
	Angus	C	.57	Winder *et al.* (1990)
Post-yearling weight				
	Mashona (18 mo)	C	.56 ± .16	Tawonezvi (1989b)
	Romosinuano (18 mo)	C	.56 ± .24	Tewolde (1988)
	Romosinuano (24 mo)	C	.86 ± .30	Tewolde (1988)

[1]   :   Abbreviations as for table 2.3 and 2.6 .

[2]   :   See Trail (1971) and a review by Preston and Willis (1974) and Plasse (1978) for earlier r_g estimates.

2.4.2.3.2 *Weaning weight and yearling and post-yearling weight*

Woldehawariat *et al.*, 1977 (cited by Thrift *et al.*, 1981) summarized the genetic correlation estimates between weaning weight and yearling weight of beef cattle and found an average value of .71. Plasse and Verde (1976) (cited by Plasse, 1978) reported a genetic correlation estimate of .92 between weaning weight and yearling weight on Brahman cattle. Recent genetic correlation estimates between weaning weight and yearling weight of beef cattle breeds are given in table 2.18.

Preston and Willis (1974) summarized genetic correlations between weaning weight and weights at the final period of performance tests in various beef cattle studies. The values ranged from .33 to .77 with an average of .53. Plasse (1978) summarized genetic correlation estimates between weaning weight and some post-yearling weights of *Bos indicus*, they ranged from .21 to .89 (an average of .72). Recent genetic correlation estimates between weaning weight and post-yearling weights of beef cattle are given in table 2.19.

In summary, the estimates of the genetic correlation between weaning weight and yearling and post-yearling weight in beef cattle are moderate to highly positive.

2.4.2.3.3 *Yearling and post-yearling weight*

Trail *et al.* (1971) reported an average value of .72 with a range from .31 to .91 of genetic correlation estimates between yearling weight and some post-yearling weights in *Bos indicus* crossbreds. Recent genetic correlation estimates between yearling weight and post-yearling weight of beef cattle are given in table 2.20.

In summary, the genetic correlation between yearling weight and some post-yearling weights in beef cattle are highly positive.

Table 2.18 **Recent paternal half-sib genetic correlation estimates between weaning and yearling weight from various studies on beef cattle [1,2].**

Breed	Sex	$r_g \pm se$	Authors
Bos indicus :			
Nellore	C	.60	Bergman *et al.* (1984)
Nellore	C	.60	Silva *et al.* (1988)
Romosinuano	C	.77 ± .14	Tewolde (1988)
Gobra	C	.93 ± .09	Sow *et al.* (1988)
Bos taurus			
Various breed	C	.61 to .8	Schaefter and Wilton (1981)
Angus	F	.76 ± .07	Alenda and Martin (1987)
Red Angus	C	.78 ± .02	Winder *et al.* (1990)
Angus	M	.79	Knights *et al.* (1984)
Angus	M	.89 ± .05	Alenda and Martin (1987)
Hereford	C	.90 ± .11	Itulya *et al.* (1987)

[1] : Abbreviations as for table 2.3 .

[2] : See reviews by Woldehawariat (1977) (cited by Trift *et al.*, 1981) and Plasse and Verde (1976) for earlier r_g estimates.

Table 2.19 Recent paternal half-sib genetic correlation estimates between weaning weight and post-yearling weight from various studies on beef cattle [1,2].

Breed	Age at post-yearling	$r_g \pm se$	Authors
Bos indicus :			
Nellore	550 d	.46	Silva *et al.* (1988)
Sanga	540 d	.47	Lubout and Swanepoel (1990)
Mashona	18 mo	$.67 \pm .12$	Tawonezwi (1989b)
Nellore	550 d	.75	Rosa *et al.* (1988)
Gobra	18 mo	$.93 \pm .11$	Sow *et al.* (1988)
Gobra	24 mo	$.62 \pm .29$	Sow *et al.* (1988)
Bos taurus :			
Hereford	20 mo	$.53 \pm .28$	DeNise and Torabi (1989)
Various breed	700 d	.85	Robinson (1990)
Various breed	550 d	.92	Robinson (1990)
Angus cross	20 mo	$.97 \pm .31$	Johnson *et al.* (1986)
Hereford	20 mo	$1.06 \pm .12$	Itulya *et al.* (1987)
Hereford	24 mo	$1.11 \pm .12$	Itulya *et al.* (1987)

[1] : Abbreviations as for table 2.3 and 2.6 .

[2] : See reviews by Preston and Willis (1974) and Plasse (1978) for earlier r_g estimates.

Table 2.20   Recent paternal half-sib genetic correlation estimates between yearling weight and post-yearling weight from various studies on beef cattle [1, 2].

Breed	Age post-yearling	$r_g \pm se$	Authors
Bos indicus :			
Gobra	24 mo	.14 ± .27	Sow *et al.* (1988)
Nellore	550 d	.59	Rosa *et al.* (1988)
Sanga	540 d	.77	Lubout and Swanepoel (1990)
Nellore	550 d	.81	Silva *et al.* (1988)
Gobra	18 mo	.84 ± .12	Sow *et al.* (1988)
Gobra	18 mo	.94	Abassa *et al.* (1990)
Bos taurus :			
Hereford	20 mo	.71 ± .14	Itulya *et al.* (1987)
Hereford	20 mo	.76 ± .25	DeNise and Ray (1987)
Hereford	24 mo	.81 ± .09	Itulya *et al.* (1987)
Angus cross	20 mo	.84 ± .10	Johnson *et al.* (1986)

[1]   :   Abbreviations as for table 2.3 and 2.6 .

[2]   :   See Trail *et al.* (1971) for earlier r_g estimates.

2.4.2.3.4 Body weight and carcass traits

Preston and Willis (1974) published the genetic correlation estimates between weaning weight and carcass grade and the average value was .75. Moreover, the average genetic correlation between the final weight on performance test and carcass grade and fat thickness were .88 and .31, respectively. Recent genetic correlation estimates between some body weight traits and carcass traits are shown in table 2.21.

In summary, there are moderate to highly positive genetic correlation estimates between body weight and carcass weight of beef cattle, but generally lower estimates for body weight and carcass quality traits.

2.4.2.3.5 Body weight and reproductive traits

Philipson (1976) reported that average genetic correlations between birth weight and gestation length, stillbirths and calving difficulties in Swedish cattle breeds were .36 (average of two values), .40 (average of two values) and .92 (average of six values ranging from .19 to .31), respectively. Burfening *et al.* (1978) found that genetic correlations between birth weight and calving ease score (from 1 for no assistance to 4 for caesarian section) and gestation length for Simmental cattle were .33 and .30, respectively and between weaning weight and calving ease and gestation length were .08 and -.02, respectively. Morris (1980) reviewed the genetic correlations between weaning weight and age at puberty and weight at puberty and noted average values of -.52 and .52, respectively. Recent genetic correlation estimates between body weight and reproductive traits are shown in table 2.22.

In summary, the genetic correlations between body weight traits and scrotal circumference are moderate to high. There is a moderate positive genetic correlation between birth weight and calving difficulties, a moderate negative estimate for that between weights and age at puberty and a moderate to high estimate for that between weaning weight and weight at puberty. Genetic correlations between birth weight and stillbirths are highly positive.

Table 2.21 Recent paternal half-sib genetic correlation estimates between body weight and carcass traits from various studies on beef cattle [1,2].

Carcass Traits	Body weight at			Breed	Sex	Authors
	Weaning	Yearling	Post-Yearling (age)			
Carcass weight :						
yearling	.52±.21	-	-	Herdford cross	C	Wilson *et al.* (1976)
yearling	-	.60	-	Herdford	H	Blackwell *et al.* (1962)
31 mo	-	-	.91 (31 mo)	Various	M	Morris *et al.* (1990)
	-	-	.93	Friesian cross	M	More O'ferall *et al.* (1989)
434 d	.90	.95	-	Hereford	M	Shelby *et al.* (1963)
yearling	-	-	.96	Hereford	M	Lamb *et al.* (1990)
20 mo	.77	.81	.97 (2o mo)	Angus cross	S	Johnson *et al.* (1986)
422 d	.48±.25	.96±.03	-	Hereford	F	Koch (1978)
20 mo	-	-	1.00 ± .01 (20 mo)	Various	M	Morris *et al.* (1990)
Dressing % :						
20 mo	-.37	.05	.01 (2o mo)	Angus cross	S	Johnson *et al.* 1986
434 d	.30	.04	-	Hereford	M	Shelby *et al.* (1963)
yearling	1.56	1.07	-	Herdford	H	Blackwell *et al.* (1962)
Fat depth :						
yearling	.13	-	-	Hereford	M	Lamb *et al.* (1990)
31 mo	-	-	-.31 (31 mo)	Various	M	Morris *et al.* (1990)
422 d	.59±.34	.86±.24	-	Hereford	F	Koch (1978)
434 d	.91	.29	-	Hereford	M	Shelby *et al.* (1963)
20 mo	-	-	-.85 (20 mo)	Various	M	Morris *et al.* (1990)
Rib eye area :						
434 d	.40	.03	-	Hereford	M	Shelby *et al.* (1963)
422 d	.16±.50	.01±.46	-	Hereford	F	Koch (1978)
yearling	.43	-	-	Hereford	M	Lamb *et al.* (1990)

[1] : Abbreviations as for table 2.3 and 2.6 .

[2] : See review by Preston and Willis (1974) for earlier r_g estimates.

Table 2.22 Recent paternal half-sib genetic correlation estimates between body weights and reproductive traits from various studies on beef cattle [1,2].

| Reproductive Traits | Body Weight at | | | | Breed | Authors |
	Birth	Weaning	Yearling	Post-yearling		
MALE :						
Scrotal circumference :						
(365 d)	.18 ± .19	.29 ± .18	.44 ± .16	-	Hereford	Bourdon and Brinks (1986)
(365 d)	-	.86 ± .15	.52 ± .34	-	Hereford	Neely *et al.* (1982)
(365 d)	-	.56	.63	-	Hereford and Angus	Smith *et al* (1989c)
(365 d)	.49	.00	.68	-	Angus	Knights *et al.* (1984)
Sperm production :						
	-	.90 ± .12	.56 ± .39	-	Hereford	Neely *et al.* (1982)
	-.47	.12	.31	-	Angus	Knights *et al.* (1984)
Percent of normal sperm						
	-	.20	.26	-	Hereford and Angus	Smith *et al.* (1989c)
FEMALE :						
Age at puberty :						
	-	-.04	-.14	-	Hereford and Angus	Smith *et al* 1989b
Gestation length						
	.45	-	-	-	Various *Bos taurus* breeds	Cundiff *et al.* (1986)
	.49	-	-	-	Simmental	Hagger and Hofer (1990)
	.57	-	-	-	Black and White Swiss	Hagger and Hofer (1990)
	.59	-	-	-	Braunvieh	Hagger and Hofer (1990)

table 2.22 (continued)

Age at first calving :					
-	-.22 ± .41	-.17 ± .40	-	Hereford, Angus	Bourdon and Brinks (1982)
Calving difficulty :					
.61±.09	-	-	-	Various *Bos taurus* breeds	Cundiff *et al.* (1986)
.92	-	-	-	Braunvieh	Hagger and Hofer (1990)
.93	-	-	-	Black and White Swiss	Hagger and Hofer (1990)
.93	-	-	-	Simental	Hagger and Hofer (1990)
Stillbirth					
.55	-	-	-	Braunvieh	Hagger and Hofer (1990)
.68	-	-	-	Black and White Swiss	Hagger and Hofer (1990)
.72	-	-	-	Simental	Hagger and Hofer (1990)
Calf survival					
-.49 ± .19	-	-	-	Various *Bos taurus* breeds	Cundiff *et al.* (1986)

[1] : abbreviations as for table 2.6 .

[2] : see reviews by Phillipson (1976), Burftening (1978) and Morris (1980) forPlasse (1978) for earlier r_g estimates between body weight and female reproductive traits.

2.4.3. Factors influencing the magnitude of phenotypic and genetic parameters

Results of studies reviewed here indicate that estimates of phenotypic and genetic parameters for any particular trait or trait combination show considerable variation in beef cattle. Several factors may contribute to the variation in the value of parameter estimates.

Increasing the environmental variation could decrease heritability estimates. Field data have more environmental variation than experimental data so the first situation may undervalue the heritability estimate (Kennedy and Henderson, 1975a). Itulya *et al.*, (1987) reported heritability estimates of weaning weight for Hereford cattle of .05 ± .03 and .18 ± .05 for males and females, respectively. They noted that the lower values may have been due to increased environmental variation as a consequence of inadequate nutrition and other stresses. The female heritability estimate for the weaning weight was higher than that for males and might be a consequence of the heifers' physiological age at weaning being more conducive to the genetic expression of differences. As a result, males might be more sensitive to a sparse nutritional environment. DeNise *et al.* (1988) found heritability estimates of weaning weight for Herefords in good and poor conditions were .37 ± .10, and .21 ± .08, respectively. Heritability estimates of Hereford bull yearling weight in good and poor environments were .58 ± .15 and .32 ± .12, respectively (DeNise and Torabi, 1989). They suggested that the reduction in heritability from good to poor conditions was due to an increase in environmental variation. Lubout and Swanepoel (1990) observed a heritability of .05 ± .04 for weaning weight in Sanga cattle and indicated that this small value was due to a large environmental effect on the performance of animals.

Environmental variation experienced by an animal during it's growth is the main factor affecting the magnitude of the phenotypic and genetic correlation between

two characters. Compensatory growth of individuals during post-weaning may cause a downward bias of the phenotypic covariance between weaning and yearling traits (Franscoise *et al.*, 1973, Kennedy and Henderson, 1975b). DeNise and Torabi (1989) studied Hereford bulls in a stressful environment and reported that the phenotypic correlation between weaning and yearling weight for good years was higher than for poor years. Animals with the better pre-weaning environment were more affected by a poor post-weaning environment. Kennedy and Henderson (1975b) in a study with Aberdeen Angus calves noted that estimates of the genetic correlation seemed to be more affected by sampling errors than the phenotypic correlation between traits for either field or experimental data.

Phenotypic and genetic parameter estimates might be lower due to a large proportion of unexplained residual variance due to the model used to represent the data. Oni *et al.* (1990) found the heritability estimate for weaning weight based on the regression of offspring on parents of Bunaji cattle was .11 ± .19. They indicated that this low value might be due to the inadequacy of the model to explain most of the variation of body weight. A large proportion of unexplained residual variation would lead to an inflation of error variance and thus a lower estimate of heritability (Oni *et al.*, 1990).

Ideally, to minimize environmental variation, animals should be treated to similar conditions. From the practical point of view, all non-genetic effects should be recorded and adjusted for or included in the statistical model analysis before estimating genetic variance components. The use of Best Linear Unbiased Prediction (BLUP) is another suggested way to minimize various possible environmental variation as this method is able to adjust for various non-genetic effects and yield the minimun error variance components. BLUP is the preferred method if selection is across age-groups and across herd (Garrick, 1991). It provides a powerful means of estimating the breeding merit as it makes an approach to real life situations in allowing for the unequal distribution of progeny of a sire across herds, for the continual selecting of a population and provides a

means of estimating the genetic merits of animals when generations are overlapping (King, 1989).

Effects of selection on the genetic parameter estimates may be a possible explanation for the low value obtained (Van Vleck, 1968, Henderson, 1975, Roberston, 1977, Rothschild *et al.*, 1979, Johnson and Notter, 1987, Gomez-Raya and Burnside, 1990, Mayo *et al.*, 1990 and Famula and Van Vleck, 1990). Barlow and Dettman (1978) observed a lower heritability estimate for weaning weight of Angus cattle in their study as a possible result from selection. Trift *et al.* (1981) found that the heritability estimates for weaning weight for control male and female populations were 1.3 and 2.4, respectively, times larger than estimates from selected populations. They also observed that the heritability estimates of yearling weight for unselected animals was 3.0 or 3.5 larger than that of selected males and females, respectively. Wilson *et al.* (1986) who examined variance components and heritabilities from field records for Angus and Hereford noted that the lower heritability estimates for weaning weight (.13 and .16 for Hereford and Angus, respectively) and for post-weaning weight might be due to the selection programs undertaken for several years in the herds studied. Selection might have reduced the amount of genetic variation (Curnow, 1964) which in turn resulted in lower genetic parameter estimates. The greatest impact of artificial selection in reducing variance is in the second generation of selection. It will reduce more slowly in later generations until a limit is reached due to the opposing force of natural selection (Falconer, 1981). However, there is the chance that selection may cause a geater change in variance if there is a joint action of artificial and natural selection (Falconer, 1981).

Biased parameter estimates due to selection could be decreased by including all information on relationships in an animal model as it will account for gametic disequilibrium (Van de Werf and de Boer, 1990). Including additional relationships between animals will also adjust for inbreeding and for covariances between animals (Van de Werf and de Boer, 1990). Robertson (1977) suggested

the calculation of corrected estimates of genetic parameters (heritability and genetic correlation) for selected population. Heritability estimates obtained from collateral relative information in the selected generation would be :

$$h^2_s = h^2 (1 - K),$$

where : $\qquad K = i (i - x),$

h^2_s = corrected heritability due to selection,

h^2 = uncorrected heritability,

x = the abscissa of the unit normal curve corresponding to the proportion of individual selected, and

i = the mean value of the distribution above the point x.

The magnitude of adjusted genetic correlations would be :

$$r_{g'} = r_g - [\{ Kh^2 (1 - r^2_g) \} / 2]$$

where :

$r_{g'}$ = the adjusted genetic correlation, and

r_g = the unadjusted genetic correlation.

The number of sires used in generating field records from which genetic parameters are derived could be another possible cause of the bias. Wilson *et al.* (1986) noted that if the field records were not a representative sample of the entire breed, the sire variance could be significantly reduced. Since field records constitute only a sample of the total breed population, it could significantly reduce the sire variance and as a result the estimated heritability might be biased downward (Wilson *et al.*, 1986). In other cases, confounding of sires among other main effects may also bias the heritability estimates. Bourdon and Brinks (1982) noted that a confounding of sires within main effects will bias the sire variance components upwards, which in turn will increase the heritability estimate. Oni *et al.* (1989) reported that low phenotypic correlations among body weight traits of Bunaji cattle were possibly due to the confounding of sires within herd.

Misidentification of progeny to a sire will reduce the estimates of the genetic variance which in turn will result in an underestimate of the heritability. However,

it will not influence correlation estimates between characters as the estimated covariance and variance components of two traits will be equally biased (Christensen *et al.*, 1982). The reduction of the actual heritability estimates are about the square of the proportion of animals with correct sire identification (Van Vleck, 1970). In a large population, the heritability estimate resulted from misidentification of progeny to a sire is as follows:

$$h^{2'} = (p^2) (h^2)$$

where :

$h^{2'}$ = the heritability estimate due to misidentification of progeny to a sire,

p = the proportion of the correct identified progeny, and

h^2 = the actual heritability estimate.

The maximum reduction will be achieved if misidentification is equally distributed among sires (Christensen *et al.*, 1982). To reduce the bias due to misidentification, additional individuals per progeny group should be recorded. The value of extra individuals is equal to $n / (p^2 - n)$ where n and p are total progeny and correct identified progeny, respectively (Christensen *et al.*, 1982).

Positive assortative mating systems may bias heritability, phenotypic and genetic correlation estimates upwards. This mating system which matches animals who are more alike phenotypically for particular traits, increases the additive genetic variance and covariance (Barlow and Dettman, 1978, Gianola, 1982 and Kemp *et al.*, 1986). Reeve (1961) noted that heritabilities estimated through regression of progeny on mid-parent value will not appreciably affected by assortative mating as individual gene substitution effects are fairly small. This mating system is likely to cause more serious bias in the estimates through the correlation between non-additive gene effects. However, Gimelfarb (1985) pointed out that assortative mating could still introduce a substantial bias of the estimated offspring mid-parent regression value. Gimelfarb (1985) emphasized that results from Reeve (1961) were only limited for assumptions based on Fisher's model (a character is controlled by an infinite number of loci, only two alleles in each locus, no epistatic effects and the distribution of genotypic values is bivariate normal) and could not

be generalized to other situations. Reeve (1953) suggested that any heritability or genetic correlation estimate where parents were mated assortatively should be adjusted using the change of mid-parent variance of a trait.

Statistical techniques may generate different variance component estimates and in turn yield different estimates of the parameters from the same source of records, especially for unbalanced data. Furthermore, difference in computational techniques used in obtaining iterative solutions to equations can effect the final results. In the case of Henderson's Method III, different estimates will be obtained from different sets of equations to compute reductions of sums of squares. Corbeil and Searle (1976) observed that variances calculated for REML estimates are always equal to or less than the corresponding variances for Henderson's Method III. They noted that REML can be superior to ML and Henderson's Method III when there are only one or two observations per cell. Cantet *et al.* (1990) in a simulation exercise to study properties of likelihood and quadratic estimators found that REML was better than ML and confirmed the superiority of likelihood based estimators under selection as these methods outperformed quadratic methods with respect to estimated mean squared error. However, Colleau *et al.* (1989) noted that estimates of genetic parameters and sampling variances provided by Henderson's Method III may be the same as those of REML due to the number of progeny per sire beings comparatively homogeneous.

Nicholas (1987) described that paternal half-sib heritability estimates will yield a better result than others. It can be explained by establishing the resemblance between relatives, that can be expressed as :

$$\text{Resemblance} = [ah^2] + [d \{\sigma^2_D / \sigma^2_P\} + [\sigma^2_{Ec} / \sigma^2_P],$$

where a, d, σ^2_D, σ^2_P and σ^2_{Ec} are additive relationship, the probability of relatives having the same genotype, dominance variance, phenotypic variance and common environmental variance, respectively. The equation can then be rearranged as follows :

$$[\text{Resemblance} /a] = [h^2] + [(d/a)(\sigma^2_D / \sigma^2_P)] + [(1/a)(\sigma^2_{Ec} / \sigma^2_P]$$

The last expression indicates that the higher the probability of relatives having the same genotype (d) and the higher the common environmental variances then the greater the bias upward of the degree of resemblance. In half-sib relatives there is no genotype in common (d = 0) and it less likely the half-sibs experience common environments than full-sibs relatives. In full-sibs, the probability of having the same genotype is .25, so the heritability estimate will be biased upward. Heritability estimates calculated by regression will be biased upward as although there may be no probability having the same genotype (d = 0), the parents and offspring may share common environments. Therefore heritability estimates calculated by half-sib methods will present relatively better results than other methods. If genetic parameters are to be obtained by regression of offspring on parents, Reeve (1953) suggested that more accurate estimates could be obtained through mating parents assortatively. This was a consequence of a decrease in the variance of the estimated regression coefficient resulting from an increase in the variance of mid-parent values. Hill and Nicholas (1974) suggested that pooled estimates of heritability from intra-class correlation and regression would be more accurate than either the regression of offspring on parents or sib-covariance estimates alone, as pooled estimates would have less variance.

In summary, genetic parameters could be biased downwards (due to factors such as environmental variation, inappropriate model to represent data, selection, misidentification of progeny's sires and non-representative sire sample analysed) or biased upwards (due to phenotypically assortative mating systems and confounding sires among main non-genetic effects). Methods of calculation of variance components using different relationships among animals could be another possible cause of difference in estimated genetic parameters. Additionally, as different statistical methods may yield different variance and covariance component estimates, genetic parameters will then be different among techniques used.

CHAPTER THREE

ESTIMATES OF
PHENOTYPIC AND GENETIC PARAMETERS
IN BALI BEEF CATTLE

Abstract

Records on weaning (3803) and yearling weight (2990) of beef cattle (*Bibos banteng*) from the Bali Cattle Improvement Project were examined. A mixed model analysis involving all main non-genetic effects (village, year of birth, season of birth, age of dam, sex of calf, all significant interactions and age at weighing as a covariate) as fixed effects and sire nested within village as a random effect was undertaken. Variance components were estimated by Henderson's Method III and REML methods. Paternal half-sib components of variance and covariance were used to estimate heritabilities of weaning and yearling weights, as well as their genetic and phenotypic correlations. Heritability estimates obtained by Henderson's Method III for weaning and yearling weights were .11 ± .03 and .13 ± .04, respectively while the phenotypic and genetic correlations were estimated as .32 and .64 ± .10, respectively. REML estimates were similar. The parameters estimated in this study fell within the range of reported values from various breeds, but were at the lower end of the range. It is concluded that further information should be gathered to assist in estimating genetic parameters for other economic traits of Bali beef cattle and to provide more accurate estimates for weaning and yearling weights.

Introduction

The main objective of animal genetic improvement is to increase the net profit of farmers by maximizing production through an optimum use of the genetic component of the operation's output. To achieve this purpose, breeders should identify all economically traits of chosen breeds for inclusion in the selection objective. Breeds used in the tropic regions should include the native genetic resources which may have been well adapted to the environment stresses.

Bali beef cattle that were derived from the wild banteng (*Bibos banteng or Bos sondaicus*) in Indonesia are popular with Indonesian farmers because of their draught ability, high fertility, ability to thrive under poor conditions (heat, low quality of roughage) and a good dressing percentage with a low fat content. To take advantages of these traits, the Indonesian government decided to improve this tropical native cattle through establishing a Bali Cattle Improvement Project. The objectives of the project are to develop and increase Bali cattle as a valued resource, by improving their productivity through genetic selection, and to increase farmers incomes. Since 1981, New Zealand has participated in the project by assisting with the technical development of the program to produce performance and progeny-tested Bali cattle bulls. Traits to be improved include growth rate under the traditional farming system, weaning weight, yearling weight, milking ability, temperament and muscling quality. The information recorded in the program includes the pedigree of all calves, date of calving, age and weight at weighing either for weaning or yearling weight.

A number of studies have reported heritability estimates for weaning and yearling weight and correlations between them for beef cattle. Values of these parameters are generally moderate to high (Schaeffer and Wilton, 1981, Bourdon and Brinks, 1982, Alenda and Martin, 1987 and Robinson, 1990). However, there are no existing values for Bali beef cattle (*Bibos banteng*). Falconer (1981) suggested that genetic parameters for genetic improvement programmes should be

derived from the population that was to be improved. Thus, the purpose of this study is to estimate the heritability of weaning and yearling weight and their phenotypic and genetic correlations in Bali beef cattle.

Material and method

Data collection

Data was collected as part of the Bali Cattle Improvement Project during a five year period from 1983 to 1987. Records were grouped by village, year, season, age of dam and sex of calves.

Calves were born throughout the entire year. To enable a broad classification for the purposes of analysis, each year was divided into a wet season (October - March) and a dry season (April - September). A large proportion (50.0 %) of calvings occurred at the end of the dry season i.e. June to September.

The oldest dams were 7 years, as selected heifers were first mated at 18 to 24 months and were used for a maximum of 5 years. Sires were selected on the basis of growth rate from weaning to rising two year old and were only used in one village for up to two years. Therefore, it was not possible to compare villages due to the lack of genetic links.

Weaning weights of calves were recorded at a mean age of 205 days (range from 135 to 275 days) while yearling weights were recorded at an average age of 365 days (range from 276 to 455 days). 3803 paternal half-sib records from 98 sires and 2990 records from 87 sires were used to estimate the heritability of weaning and yearling weight, respectively. There were 2679 records from 87 sires available to examine the phenotypic and genetic correlation between these traits. The number of records in each class of non-genetic groups (year, season, dam age and sex) for weaning and yearling weight is shown in table 1. The number of records per village ranged from 30 to 393.

Table 1 : Number of records in each class of the non-genetic effects for weaning weight and yearling weight.

Classes		Weaning weight	Yearling weight
Year	1983	1201	1127
	1984	1049	707
	1985	666	434
	1986	496	487
	1987	390	235
Season	Dry	2523	2057
	Wet	1279	933
Dam age	2 year	128	108
	3 year	1068	897
	> 3 year	2606	1985
Sex	Bull	1966	1564
	Heifer	1836	1426

Statistical analysis

Preliminary analysis was conducted to examine non-genetic effects and their first order interaction effects. Dam-age groups were classified into 3 groups (2, 3 and more than 3 years at calving). All non-significant interaction effects (P > 0.05) were excluded from the model.

A linear mixed model analysis for weaning weight including all main effects (village, year of birth, season of birth, age of dam and sex of calf), significant interactions (village by year, village by season, year by season, year by calf sex, dam age by season and by sex of the calf) and age of the calf (covariate) as fixed effects and sire nested within village as a random effect. For yearling weight, the mixed model included the same fixed effects as for weaning weight and interactions of village by year, season of birth, age of dam and sex of the calf, sex by year of birth and age of dam and season of birth by age of dam. In both models sire and error terms were assumed to be uncorrelated random variables with zero means.

The sire nested within village and residual variance components were derived using both Henderson's Method III and REML (Restricted Maximum Likelihood Method). Henderson's Method III was preferred over Model I and II as the appropriate mixed model included interactions and fixed and random effects (Henderson, 1953 and Searle, 1989). REML was also used as it would only yield positive variance component estimates (Patterson and Thompson, 1971).

Mean squares of sire nested within village were generated by using the ANOVA procedure of the SAS computing package (SAS, 1985). Sire variance components were yielded by equating the sire (nested within village) mean square to its expected value. Variance components by REML were derived using the Varcomp procedure (SAS, 1985) after adjusting weights for age at weighing. Covariance components were calculated from analysis of the sum of weaning and yearling weight records for each individual.

Heritabilities, genetic and phenotypic correlation and their standard errors were estimated from paternal half-sib analysis following Becker (1984).

Results

Non-genetic effects

Village, year of birth, sex and age (as a covariate) of the calf significantly (P < .05) affected weaning weight. Age of dam had a small effect (P = .08) while season of birth had no significant effect on weaning weight. Village, year of birth, age of dam, sex and age of the calf as a covariate significantly (P < .05) affected yearling weight while season of birth had no significant effect. When first order interactions among fixed effects were included in the model for weaning weight, the effects such as village by year, village by season, year by season, year by sex of the calf and dam age by season and by sex of the calf were significant (P < 0.05). For yearling weight effects of village by year, season of birth, age of dam and sex of the calf, sex by year of birth and age of dam and season of birth by age of dam were significant (P < 0.05).

Least squares means ± standard error (LSM ± SE) for weaning and yearling weight by village contemporary group ranged from 79.4 ± 1.18 kg to 94.4 ± 1.08 kg and from 124.1 ± 1.7 kg to 153.8 ± 1.7 kg, respectively. The least squares mean of weaning weight for dry season born calves (85.4 ± .5 kg) was the same as that for wet season born calves (85.0 ± .5 kg). Similarly, LSM for yearling weight in dry season born calves (138.1 ± .7 kg) and wet season born calves (138.3 ± .8 kg) were similar. LSM of weaning and yearling weight for year of birth, age of dam and sex group are shown in table 2. Age at weighing as a covariable was significant (P < 0.05) for both weaning and yearling weight. Regression coefficients of weaning weight and yearling weight on the age were 0.30 kg/day and 0.20 kg/day, respectively. R-squares for appropriate non-genetic effect models for weaning and yearling weight were 67% and 62%, respectively.

Table 2 :   Least squares means (LSM) and standard errors (SE) for weaning and yearling weight based on year, dam age and sex contemporary groups [1].

Group	Subgroup	Weaning weight (kg)		Yearling weight (kg)	
		LSM	SE	LSM	SE
Year	1983	88.6[a]	.51	135.9[a]	.74
	1984	86.4[b]	.56	134.8[a]	.86
	1985	84.9[c]	.64	147.1[b]	1.03
	1986	88.3[a]	.74	137.6[a]	1.07
	1987	77.6[d]	.82	135.5[a]	1.38
Dam age	2 yo	83.9[a]	1.16	140.4[a]	1.72
	3 yo	85.4[a, b]	.43	134.7[b]	.68
	>3 yo	86.1[b]	.30	139.4[a]	.48
Sex	Bull	89.8[a]	.49	145.5[a]	.75
	Heifer	80.5[b]	.49	130.9[b]	.75

[1] : LSM with different superscripts significantly different (P < .05).

Heritabilities and Correlation

Paternal half-sib estimates of heritabilities for weaning and yearling weight by Henderson's Method III and REML are shown in table 3. The genetic correlation between weaning and yearling weight was highly positive for both methods of estimation (table 3). The phenotypic correlation between the two traits was positive but smaller than the comparable genetic correlation.

Discussion

Non-genetic effects

The most likely explanation of the significant effect of village on weaning and yearling weight of Bali cattle in the present study is the different management regimes among villages. Other studies have reported that significant herd or regions effects on production traits may reflect potential for growth capability in the calf and differences in management and feeding levels applied (Anderson and Wilham,1978 and Trail *et al.*, 1985).

The significant effect of year of birth on weaning and yearling weight of Bali cattle in the present study may indicate that management practices differ between years and / or that different feeding levels occurred due to different annual rainfall patterns. Several studies have also reported significant effects of year of birth on weaning weight (Nicoll and Rae, 1977 and Pabst *et al.*, 1977) and post-weaning weight (Baker *et al.*, 1974 and DeNise *et al.*, 1989).

Table 3 :   Paternal half-sib estimates of heritabilities ± standard errors for weaning weight (WW) and yearling weight (YW) (diagonal) and their genetic (above diagonal) and phenotypic correlations (below), using either Henderson's Method III or Restricted Maximum Likelihood (REML).

Traits	Henderson's Method III		REML	
	WW	YW	WW	YW
Weaning weight (WW)	.11 ± .03	.64 ± .10	.13 ± .04	.60 ± .11
Yearling weight (YW)	.32	.13 ± .04	.32	.17 ± .04

Season of birth appears to have a small effect on weaning and yearling weight of Bali cattle in the present study. A possible explanation of the result is the minor difference in nutritional quality and quantity of forage between seasons (wet and dry season) that is available for cows. A large number of calves were born near the end of dry season and the beginning of wet season where there might be only a little difference in quality of food supply. If sufficient observations were available at other times of the year seasonal differences may be detected. A number of studies have reported that season or month of birth might significantly affect beef cattle weaning weight (Trail *et al.*, 1985 and Rosa *et al.*, 1988). This is most likely caused by a difference in dam nutrition between seasons which in turn alters lactation yields and calf growth. Further studies are needed to investigate of effects of month or season of birth on body weights of Bali cattle.

Age of dam appears to have a smaller effect on weaning weight (P = 0.08) than on yearling weight (P < 0.01). It seems that age of dam in the present study has a lower than expected effect on milk production. Most studies of other breeds report that age of dam significantly affects weaning (Gregory *et al.*, 1978, Nicoll and Rae, 1977, Nicoll and Rae, 1978, Anderson and Wilham, 1978, 1982, Butzon *et al.*, 1980 and Buvanendran, 1990) and yearling weight (Sharma *et al.*, 1982). The less than expected effect of dam age on weaning weight may be due to different age groups receiving different management thereby masking the true differences in cow milking ability.

Sex of calf significantly affected both weaning and yearling weight of Bali cattle. The hormonal and physiological basis of this difference in growth between the sexes is well understood. Most studies have reported that calf sex had significant effects on beef cattle weaning weight (Pabst *et al.*, 1977, Sharma *et al.*, 1982, Trail *et al.*, 1985, Buvanendran, 1990) and post-weaning weight (Baker *et al.*, 1974, Nicoll and Rae, 1977, Nicoll and Rae, 1978 and Winroth, 1990).

Age at weighing as a linear covariate has a highly significant effect on both weaning and yearling weight of Bali cattle in the present study. Age at weighing controls the largest proportion of variation in both weaning and yearling weight. Most other studies have also indicated that age at weaning has a significant effect on weaning weight (Nicoll and Rae, 1977, Barlow and Dettman, 1978, Butson *et al.*, 1980 and Buvanendran, 1990) and post-weaning weight (Baker *et al.*, 1974, Nicoll and Rae, 1977 and Nicoll and Rae, 1978).

Both weaning and yearling weight of Bali cattle were significantly affected by interactions between several non-genetic effects, such as village by year, village by season, year of birth by sex of the calf, season of birth by age of dam and sex of the calf by age of dam. The most likely explanation of these interactions is the different yearly management among villages and the possibility of different seasonal distribution of rainfall between years in the region. Several studies have indicated that herd might interact with year of birth and significantly affect beef cattle weaning and post-weaning weight (Nicoll and Rae, 1978 and Trail *et al.*, 1985). Furthermore, there may be preferential treatment of different classes of stocks. Several studies have reported the interactions between year of birth by sex of the calf on weaning weight (Baker *et al.*, 1974 and Buvanendran, 1990), post-weaning growth (Tewolde, 1988) and of sex by age of dam on weaning weights (Baker *et al.*, 1974 and Sharma *et al.*, 1982).

The presence of several significant non-genetic effects, and interactions amongst those effects, emphasises the need for an effective recording scheme. All weaning and yearling weights should be adjusted for these effects when attempting to rank animals based on their genotype, thereby increasing the accuracy of selection and enhancing the rate of genetic gain.

Heritabilities

The heritability estimates for weaning weight and yearling weight in the present study tend toward the lower values quoted in the literature. The present results of heritability estimates are lower than the average of values reviewed by Preston and Willis (1974), .26 and .60 for weaning and yearling weight, respectively. The most likely explanation of low heritability estimates in the present study is the consequence of large environmental variation. In particular, this would be contributed to by the lack of genetic linkages between villages and the year round calving pattern. Field data often exhibit large environmental variation which result in the heritability estimate being underestimated (Kennedy and Henderson, 1975a). Lubout and Swanepoel (1990) reported a low heritability of weaning weight in Sanga cattle due to a large effect of the environment on the performance of animals. Large unexplained environmental effects result in linear models that are inadequate in explaining variation in the data. R-square values of models for weaning and yearling weight in the current analysis are 67% and 62%, respectively. Oni *et al.* (1990) also found low heritability estimates for body weight in Bunaji cattle and suggested the model was inadequate to explain most of the variation of body weights. A large proportion of unexplained residual variation leads to an inflation of error variance and thus decreases heritability estimates.

Heritability estimates for both weaning and yearling weight in the present study yielded by Henderson's Method III and REML are similar. Other studies have also reported that similar estimates of the parameters yielded by Henderson's Method III and REML would be expected if there was no selection operating on the population (Knights *et al.*, 1984, Lin and McAllister, 1984 and Hayes and Cue, 1986). Colleau *et al.* (1989) noted that estimates of genetic parameters and sampling variances provided by Henderson's Method III might be similar to those of REML if the number of progeny per sire was relatively homogeneous.

However, REML is the preferred method if selected populations are to be analysed (Henderson, 1986).

Correlations

The positive phenotypic and genetic correlation estimates between weaning and yearling weights in this study fall within the range of the various literature values (Schaeffer and Wilton, 1981, Bourdon and Brinks, 1982, Alenda and Martin, 1987 and Robinson, 1990). However, the values obtained are at the lower end of these ranges. The lower correlation estimates in this study are also likely to be caused by the large environmental variation due to the problems suggested previously. Furthermore, compensatory growth of individuals during the post-weaning stage may cause a downward bias of the phenotypic covariance between weaning and yearling weights (Franscoise *et al.*, 1973 and Kennedy and Henderson, 1975b). DeNise and Torabi (1989) also reported that the phenotypic correlation between weaning and yearling weight might be low in poor conditions due to the stressful environment experienced by animals.

Genetic correlation estimates between weaning and yearling weight yielded by Henderson's Method III are similar to those by REML. The population studied has been undergoing selection for only 5 years and several reports have suggested that the parameter estimates yielded by Henderson's Method and REML would be similar under these conditions (Lin and McAllister, 1984 and Hayes and Cue, 1986).

Implications for genetic improvement

Genetic parameters obtained from this study can be utilised for further improvement of selection programs in the Bali Cattle Improvement Project. Low heritability estimates for both weaning and yearling weights suggest a need to

improve the model specification in an attempt to account for more environmental variation. However, the adequate genetic variation in both weaning and yearling weights indicates that selection for both traits is justifiable. Moreover, the existence of favourable genetic correlation between two traits also indicates that selection for weaning weight alone should also improve yearling weight of Bali cattle. For future improvement of Bali beef cattle, there is a need to collect information on traits such as birth weight and rising two year old weights, reproduction traits, carcass traits and feed efficiency so their phenotypic and genetic parameters can be estimated. These parameters are needed for the construction of a selection index which will maximise the response to selection in all the economically important traits.

CHAPTER FOUR

SELECTION INDEX

4.1. Introduction

A selection index can be defined as a linearly-weighted function of observations on an animal and or its relatives for one or more traits, in order to select those animals expected to have the highest aggregate breeding value (Hayes and Hill, 1980). The selection index method can be used for various purposes such as to select an animal based on two or more traits whose information was able to be derived either from an individual only or from its relatives (Henderson, 1963). Moreover, using the selection index would be advisable if the traits concerned have low heritability estimates (Hazel and Lush, 1942). In this case, the selection index is able to combine various sources of information to maximize the correlation between the true breeding value and an index.

The present chapter discusses theoretical procedures of deriving a selection index and calculating response to selection and demonstrates examples related to Bali beef cattle.

4.2. Constructing a selection index.

There are several steps in constructing a selection index : define the selection objective, choose selection criteria and finally obtain weighting factors (based on heritabilities, correlations and relative economic values) that express the relative importance among traits included in the selection criteria.

The main goal of determining selection objectives of commercial farms is to improve the overall net profit by utilizing all sources of income and accounting for

all expenditures. Therefore, farmers or breeders should firstly be able to list all important economic characters whether they are cheap or expensive or even impossible to measure on the animals (Nicholas, 1987). For beef cattle improvement programs, selection objectives may include characters such as adaptation to the environment, low maintenance, early puberty, fertility, easy calving, maternal ability, productive longevity, efficient growth, dressing percentage and desirable carcass (Cartwright, 1982).

After deciding important economic characters, the next step is to determine the net economic value for each trait in the selection objective. There are several methods for estimating economic values (Harris, 1970). Smith *et al.* (1986) and Ponzoni (1988b) concluded that the estimated economic value based on the ratio (income per expense and expense per income) would be a more appropriate basis than that of the profit (a difference between income and expense) as the former accounted for fixed costs. However, estimation of economic values for traits of importance is difficult as they are sensitive to production circumstances (Groen, 1990).

The overall merit (aggregate breeding value) or selection objective can be written as :

$$H = \mathbf{v}'\,\mathbf{a}$$

where :

H is the selection objective,

$\mathbf{v}$ is a vector of m by 1 economic values, and

$\mathbf{a}$ is a vector of m by 1 breeding values for individual traits in the objective.

The next step in constructing the selection index is to determine the selection criteria that is which characters will be measured as clues to improve the aggregate breeding value, by utilising their correlation with traits in the selection objective. For instance, to improve the carcass weight, the selection criterion chosen could be yearling weight as they have a moderate to high genetic correlation. Practically,

selection criteria may be different from traits in the selection objective and the number of criteria may be greater than, equal to or less than the number of traits in the objective. In general, characters employed as selection criteria should be easily and cheaply measured and have a good correlation with the selection objective. If **x** is an n by 1 vector of selection criteria and **b** is an n by 1 vector of weighting factors, the index, I, is given by :

$$I = b'x \ .$$

The final step of constructing a selection index is to derive the weighting factors expressing the relative importance of each trait in the selection criteria. In deriving weighting factors (b's), the choice of these values is to maximize the correlation between the aggregate selection objective, H, and the aggregate selection index, I (r_{HI}) as the higher the correlation the higher the efficiency of an index (Falconer, 1981). To derive weighting factors, it requires parameters such as the phenotypic standard deviation and the heritability for each trait in the selection objective and selection criteria, phenotypic correlations of each pair of the selection criteria traits and genetic correlations of each pair combination of the selection objective traits and selection criteria traits. Another parameter is the net economic value for each trait in the selection objective. These parameters are then incorporated into a set of normal simultaneous equations which will maximize r_{HI}. From a number of simultaneous normal equations (one equation for each selection criteria trait), the value of weighting factors can then be derived. In matrix notation, normal equations can be written as :

$$Pb = Gv$$

where :

P is an n by n matrix of variance-covariance of phenotypic value among n selection criteria,

b is an n by 1 vector of weighting factors,

G is an n by m matrix of variance-covariance between breeding values for the n selection criteria and the m selection objective traits, and

        v   is an m by 1 vector of relative economic values.

The weighting factors can be obtained by solving :

$$b = P^{-1} G v .$$

4.3. Response to Selection

Implementation of selection index has been proved to yield the maximum genetic progress per unit of time compared with tandem (selection for one trait only until final improvement is obtained before starting the next trait) and independent culling levels (selection based on a certain level of merits without concern for either superiority or inferiority of other traits) (Hazel and Lush, 1942, Young, 1961). The superiority of the index method increases with an increasing number of traits under selection and its superiority being at a maximum when the traits are of equal importance (Young, 1961). Regarding selection intensity, the superiority of the index method over independent culling levels decreases with increasing selection intensity, however, its superiority over tandem method is independent of selection intensity (Young, 1961).

The response to selection is the mean breeding value of the selected parents that is predicted from the regression of genetic merit on index values (Falconer, 1981). The response to selection (R) by implementing a selection index (I) can be estimated as (Falconer, 1981) :

$$R = i \, r_{HI} \, \sigma_A$$

and

$$r_{HI} = \sigma_I / \sigma_A$$

where :

         i is the selection intensity,

         r_{HI} is the correlation between the aggregate breeding value and index values,

         σ_A is the additive genetic standard deviation of the objective, and

         σ_I is the standard deviation of the index value.

In a genetic improvement program, there might be some economic traits which should be maintained at an optimum level (desirable level) but are correlated with other economic traits (Van Vleck, 1974 and Brascamp, 1984). For example, to maintain the optimum level of fat content that has a high positive genetic correlation with body weight and carcass weight. A selection program to increase the carcass weight may lead to an increase of fat content. In this case, a restricted selection index (which increases the genetic merit of one trait, for example, carcass weight, while keeping another trait, for example, fat content, unchanged) may be needed.

4.4. An example for Bali Cattle

4.4.1. Selection objectives and criteria

The main goal of the genetic improvement of Bali cattle is to increase the net income of farmers through maximizing beef production. For a long term improvement program, potential traits for a selection objective are listed in table 4.1. Ideally, all these characters should be accounted for to assist in improving the overall net profit through the implementation of a selection index. To derive a selection index, each trait in the selection objective can be improved indirectly through its corresponding selection criteria as shown in table 4.1. Given the traits listed in table 4.1, it is currently impossible to generate a complete selection index for Bali beef cattle due to many of the required parameters being unavailable. Therefore, it is only possible to construct a simple selection index based on traits for which parameters from this study or other literature are available.

Producing a high carcass weight and reducing or maintaining of the fat content of carcasses are likely to be major items of a selection objective for Bali beef cattle. Considering both breeding values for carcass weight (CW) and fat depth (FD) as items of the selection objective, the aggregate selection objective (H) can then be written as :

Table 4.1 List of traits for inclusion in the selection objective and selection criteria for a long term breeding program in Bali cattle.

Selection objectives	Selection criteria
1. Male fertility (female's pregnancy rate)	1. Scrotal circumference
2. Female fertility :	
2.1. age at first calving	2.1. weaning weight, yearling weight
2.2. pregnancy at ± 85 days post-partus	2.2. calving date
2.3. survival / longevity	2.3. birth weight, weaning weight
2.4. maternal ability	2.4. birth weight, weaning weight
3. Growth rate	3. yearling weight
4. Disease resistance	4. weaning weight, yearling weight
5. Feed efficiency	5. yearling weight
6. Weight at rising two year old (± 18 month weight)	6. yearling weight
7. Carcass weight	7. yearling weight
8. maintaning of current fat levels	8. yearling weight, fat depth

$$H = a_1 CW + a_2 FD$$

where :

$a_1 (a_2)$ = relative economic value for CW (FD).

Determining economic values for traits in the selection objective is a difficult matter. Groen (1990) described that economic values of cattle production traits were sensitive to production circumstances. Incorrect prediction of production circumstances might lead to sub-optimum weighting of traits within the selection objective (Groen, 1990). Incorrect prediction of production circumstances can be a result of uncertainty future for circumstances. In the absence of economic values for traits such as carcass weight and fat depth in Bali cattle, it will be assumed that an increase of 1 kg carcass weight of Bali cattle will result in a payment increase of $ 3 payment and for every 1 mm increase in carcass fat depth there will be a payment reduction of $ 5. Thus, with a_1 and a_2 being 3 and -5, respectively, the first selection objective (H_1) can be written as :

$$H_1 = (3) CW + (-5) FD.$$

The second selection objective (H_2) will be to increase carcass weight while keeping fat depth unchanged.

As there will be difficulties in measuring of carcass weight and fat depth in live animals and weaning and yearling weight have good genetic correlations with carcass weight and fat depth, they are reasonable selection criteria for achieving the chosen selection objective. They can then be formulated into several indices as follows :

$$I_1 = b_1 WW ,$$
$$I_2 = b_2 YW, \text{ and}$$
$$I_3 = b_1 WW + b_2 YW ,$$

where :

I_1, I_2, I_3 = selection index based on weaning and / or yearling weight,

WW = deviation from group mean for adjusted weaning weight,

YW = deviation from group mean for adjusted yearling weight, and,

$b_1(b_2)$ = weighting factor for WW (YW).

A fourth index (I_4) will be formulated to meet the objective of no genetic change in fat depth.

4.4.2. Required parameters

There were no available estimates of the phenotypic standard deviation of fat depth, fat content, phenotypic and genetic correlations between body weights (weaning and yearling weight) and carcass traits (carcass weight and fat depth) in Bali beef cattle. As a consequence, estimates of these parameters from other breeds were utilised to enable the above selection index examples to be examined. The phenotypic standard deviation for fat depth was obtained from the Brahman breed (Abraham *et al.*, 1968) while heritability estimates (carcass weight and fat depth) and genetic correlations (selection criteria and selection objective traits) are average values from table 2.7 and 2.21, respectively. Parameters used are shown in table 4.2.

4.4.3. Selection index and response to selection

Weighting factors and response to selection were derived by using the SELIND computer package (Cunningham, 1970). The main index, correlation between breeding values and the index values, variance of index values, variance of breeding values and the response to selection based on present assumptions of economic values are shown in table 4.3.

Table 4.2 Relative economic value (REV), phenotypic standard deviation (SD), heritability (on diagonal), phenotypic correlation (above diagonal) and genetic correlation (below diagonal) for selection objective traits (CW = carcass weight and FD = fat depth) and selection criteria (WW = weaning weight and YW = yearling weight).

Main concerns	Traits	REV ($)	SD	Heritability and correlations			
				CW	FD	WW	YW
Selection objectives	CW	3	27.66 (kg)[2]	.40[3]			
	FD	-5	5 (mm)[4]		.45[3]		
Selection criteria	WW		11.24[1]	.67[3]	.54[3]	.11[1]	.32[1]
	YW		14.40[1]	.83[3]	.58[3]		.13[1]

Notes:
[1] : Values based on results of the present study.
[2] : An average value for Bali cattle reviewed by Payne and Rollinson (1973) and Subandryo *et al.* (1979).
[3] : An average of values from table 2.7 and 2.21.
[4] : A value from Abraham *et al.* (1968).

Table 4.3 Weighting factors, correlations between objective [1] and index, standard deviation of the index and objective and the response to selection for 4 selection indices

Items	Index			
	$I_1 = 0.77$ WW	$I_2 = 0.85$ YW	$I_3 = 0.47$ WW $+ 0.72$ YW	$I_4 = -0.13$ WW $+ 0.09$ YW [2]
Standard deviation	8.66	12.20	13.19	1.64
Standard deviation of aggregate genotype	52.64	52.65	52.65	52.65
Correlation between index and objective (r_{HI})	0.16	0.23	0.25	0.03
Response to selection [3]				
Objectives ($)	8.66	12.20	13.19	1.64
Carcass weight (kg)	3.89	5.23	5.73	0.55
Fat depth (mm)	0.60	0.70	0.80	0.00
Weaning weight (kg)	1.24	0.90	1.21	- 0.43
Yearling weight (kg)	1.15	1.87	1.95	0.41

[1]: H = (3) CW + (-5) FD)

[2]: I_4 = restricted index; no genetic change in fat depth.

[3]: Per generation assuming one unit of standardised selection differential.

Results from table 4.3 show that a selection index considering both weaning and yearling weight (I_3) will result the greatest responses to selection (per generation) in individual traits and also in the objective gain ($ 13.19). This is reasonable as the use of more than one trait for selection criteria will increase the accuracy of the selection index. The selection index of yearling weight (I_2) yielded a higher response than selection for weaning weight (I_1) alone. It is likely to be due to the higher correlation coefficients between the selection objective and yearling weight than between the objective and weaning weight. The small difference in economic gain between I_3 and I_2 might indicate that selection on yearling weight alone can be considered for attaining the present objective. Restricting the index so that fat depth was held constant resulted in very poor economic gains ($ 1.64). This would suggest the current economic value for fat depth would have to substantially larger before consideration of a restricted index would be worthwhile.

4.5. Conclusions

The above discussion indicates that a selection index for weaning and yearling weight gives increases in both carcass weight and fat depth but increases in fat depth do not offset the increased payment for carcass weight. As there are positive genetic correlations between birth weight and weaning and yearling weight, the selection index may also increase birth weight which may then increase calving difficulties. The use of a restricted index for keeping fat depth unchanged does not seem to be worthwhile, this is likely due to a relative low economic value for fat depth. To increase the accuracy of the selection index, it is necessary to obtain relative economic values of traits in the selection objective which are more relevant to the future economic returns to be obtained from Bali cattle. Adding of other economically important traits to the selection objective is suggested so as to more accurately reflect the desired type of Bali cattle. This will required estimates of heritabilities, phenotypic and genetic correlations for other traits of importance. Revised indices will need to be generated as new information derived from Bali beef cattle becomes available.

CHAPTER FIVE

GENERAL DISCUSSION AND CONCLUSIONS

Analysis of data collected as part of the Bali Beef Cattle Improvement Programme indicates that village has a highly significantly effect on weaning and yearling weight of Bali cattle. The most likely explanation of this result is the different management regimes among villages. Anderson and Wilham (1978) reported that weaning weight was different between regions due to the management applied. Trail *et al*. (1985) showed that area of ranch had significant effects on cow productivity of Boran cattle due to different treatments. Studies on Nellore cattle in various regions of Brazil showed that herd significantly affected weights at weaning, yearling and post-yearling (Rosa *et al*., 1988 and Oliveira and Duarte, 1989). Various studies have indicated that significant herd effects on production traits may reflect potential for growth capability in the calf and differences in management and feeding levels applied. Since village has significant effects on weaning and yearling weight, animals should be genetically ranked within village. If animals are to be ranked across village, sires should be used in several villages to provide genetic links and BLUP methodology should be used to predict animal breeding values. Similar management for all groups of animals would also be beneficial in reducing between village variation.

Weaning and yearling weight of Bali cattle in the present study were also significantly affected by year of birth. These results may indicate that management practices differ between years and / or that different feeding levels occurred due to different annual rainfall patterns. Results of most studies have reported significant effects of year of birth on weaning weight (Singth *et al*., 1970, Martojo, 1975, Nicoll and Rae, 1977, Pabst *et al*., 1977 and Itulya, 1977) and post-weaning weight

(Chapman *et al.*, 1972, Baker *et al.*, 1974, Cardellino, 1988 and DeNise *et al.*, 1989). The results of the present study suggest that animals should be genetically ranked within year of birth unless genetic links exist between years which enable the genetic and environmental effects to be separated. The use of BLUP methodology would be beneficial in assisting with estimating breeding values across years.

Season of birth appears to have a small effect on weaning and yearling weight of Bali cattle in the present study. A possible explanation of the result is the minor difference in nutritional quality and quantity of forage between seasons (wet and dry season) that is available for cows and calves. A large number of calves were born near the end of dry season and the beggining of wet season where there might be only a little difference of quality of food supply. If sufficient observations were available at other times of the year seasonal differences may be detected. A number of studies have reported that season or month of birth might significantly affect beef cattle weaning weight (Trail *et al.*, 1985, Cardelino and Castrol, 1988 and Rosa *et al.*, 1988). This was most likely caused by a difference in dam nutrition between seasons which in turn altered lactation yields and calf growth. Brown *et al.* (1972) noted that breeds which showed a lack of a significant effect of month of birth on post-weaning weight indicated an occurrence of compensatory growth. The influence of season of birth on body weight decreased as the age of calves increased which was consistent with there being compensatory growth (Brown *et al.*, 1972). However, several reports have shown season or month of birth to significantly effect post-weaning weight (Presinger and Kalm, 1988 and Ordonez *at al.*, 1984). In these trials, compensatory growth presumably did not occur. Further studies are needed to investigate of effects of month or season of birth on body weights of Bali cattle. The present results suggest that for genetic merit purposes calves can be ranked regardless of the season of birth.

Age of dam appears to have a smaller effect on weaning weight ($P = 0.08$) than on yearling weight ($P < 0.01$). Since the effect of age of dam on weaning weight is

caused mainly by differences in milk production (Rutledge *et al.*, 1971, Notter *at al.*, 1978 and Robison *et al.*, 1978), it seems that age of dam in the present study has a less than expected effect on milk production. Most studies of other breeds report that age of dam significantly effects weaning ((Rhodes *et al.*, 1970, Rutledge *et al.*, 1971, Smith *et al.*, 1976, Gregory *et al.*, 1978, Nicoll and Rae, 1977, Nicoll and Rae, 1978, Anderson and Wilham, 1978, Leington *et al.*, 1982, Butzon *et al.*, 1980, Elzo *et al.*, 1987, Cardellino, 1988 and Buvanendran, 1990), post-weaning (Bair *et al.*, 1972, Young *et al.*, 1978 and DeNise and Torabi, 1989), yearling (Sharma *et al.*, 1982, Rosa *et al.*, 1988 and Oliveira and Duarte, 1989) and post-yearling weight (Nicoll and Rae, 1978 and Raymond *et al.*, 1980 and Tewolde, 1988). The less than expected effect of dam age on weaning weight deserves further study as in the future it may be desirable to separate weaning weight into maternal and direct components. It may be that different age groups are receiving different management thereby masking the true differences in cow milking ability.

Sex of calf significantly affected both weaning and yearling weight of Bali cattle. The hormonal and physiological basis of this difference in growth between the sexes is well understood. Most studies have reported that calf sex had significant effects on beef cattle weaning weight (Jeffery *et al.*, 1971, Koch *et al.*, 1973, Pabst *et al.*, 1977, Plasse, 1978, Sharma *et al.*, 1982, Trail *et al.*, 1985, Ahunu and Makarechian, 1986, Buvanendran, 1990, Leington *et al.*, 1982, Naves and Vallee, 1990 and Winroth, 1990) and post-weaning weight (Singth *et al.*, 1970, Rodhes *et al.*, 1970, Baker *et al.*, 1974, Nicoll and Rae, 1977, Nicoll and Rae, 1978, Anderson and Wilham, 1978, Tonhati *et al.*, 1986 and Winroth, 1990). Since selection normally occurs within sex, adjustment for this non-genetic effect is unimportant. However, if it becomes desirable to select for maternal performance, adjustment for sex of calf will be necessary.

Age at weighing as a linear covariate has a highly significant effect on both weaning and yearling weight of Bali cattle in the present study. Age at weighing controls the largest proportion of variation in both weaning and yearling weight.

Most other studies have also indicated that age at weaning has a significant effect on weaning weight (Singth *et al.*, 1970, Jeffery *et al.*, 1971, Baker *et al.*, 1974, Nicoll and Rae, 1977, Barlow and Dettman, 1978, Butson *et al.*, 1980 and Buvanendran, 1990) and post-weaning weight (Baker *et al.*, 1974, Nicoll and Rae, 1977 and Nicoll and Rae, 1978). Thus, it is clearly necessary to adjust both weaning and yearling weights of Bali cattle before predicting the genetic merit of various animals.

Both weaning and yearling weight of Bali cattle were significantly affected by interactions between several non-genetic effects, such as village by year, village by season, year of birth by sex of the calf, season of birth by age of dam and sex of the calf by age of dam. The most likely explanation of village by year and season of birth interactions seems to be the different yearly management among villages and the possibility of different seasonal distribution of rainfall between years in the region. Several studies have indicated that herd might interact with year of birth and significantly affect beef cattle weaning and post-weaning weight (Chapman *et al.*, 1972, Martojo, 1975 and Nicoll and Rae, 1978). Trail *et al.* (1985) reported a significant interaction effect between area and season of birth on weaning weight of Boran cattle, which was presumably due to different seasonal rainfall among areas. Different abilities between male and female calves and among ages of cows to utilise all available environmental resources which may vary due to seasonal and yearly food supply is a likely explanation of significant interactions of year by sex, season by age of dam, sex by age of dam on weaning and yearling weight. Furthermore, there may be preferential treatment of different classes of stock. Several studies have reported the interactions between year of birth by sex of the calf on weaning weight (Srinivasan and Martin, 1970, Baker *et al.*, 1974 and Buvanendran, 1990), post-weaning growth (Tewolde, 1988) and of sex by age of dam on weaning weights (Martojo, 1975, Baker *et al.*, 1974, Anderson and Wilham, 1978 and Sharma *et al.*, 1982).

Yearling weight is also significantly affected by interactions of between several non-genetic effects, for example, village by age of dam and village by sex of the

calf. Since age of dam itself has no significant effect on weaning weight, important interactions between village and age of dam and sex of calf on yearling weight may reflect a preferential treatment of cow age groups or sex groups. Rhodes *et al.* (1970) noted that management by sex interaction effects on Angus and Hereford body weights might indicate an inconsistent difference among sexes for different feeding system. It is important to emphasize that all significant interactions among non-genetic effects on weaning and yearling weight should be accounted for when attempting to rank animals based on their genotype, thereby increasing the accuracy of selection and enhancing the rate of genetic gain.

Heritability estimates of weaning weight and yearling weight for Bali cattle in the present study appear to be lower than those reported for other breeds. Field records from populations that have been operating selection programs for several years may cause lower heritability estimates. Wilson *et al.* (1986) reported that field records from populations being selected might exhibit reduced additive genetic variation. However, the current trial has only been operating for 5 years and it is unlikely that the additive genetic variance has declined. It is more likely that since the records being examined are from field data, that an increased level of environmental variation causes the low heritability values. Kennedy and Henderson (1975a) confirmed that field data contained more environmental variation than experimental data, so it is likely that the first situation would undervalue the heritability estimate. Itulya *et al.* (1987) reported low weaning weight heritability estimates which may have been due to increased environmental variation as a consequence of inadequate nutrition and other stresses. DeNise *et al.* (1988) found heritability estimates of weaning weight for Herefords in good and poor conditions were .37 ± .10, and .21 ± .08, respectively. Heritability estimates of Hereford bull yearling weight in good and poor environments as .58 ± .15 and .32 ± .12, respectively (DeNise and Torabi, 1989). They suggested that the decrease of heritability from the good to poor conditions was due to an increase in environmental variation. Lubout and Swanepoel (1990) observed a heritability of .05 ± .04 for weaning weight in Sanga cattle and indicated that this small value was

due to a large effect of the environment on the performance of animals. Low heritability values are of concern since the expected rate of response to selection will be reduced. Therefore, it would be of value to determine what other factors are contributing to the environmental variation. If these can be identified, it may be possible to adjust the data to increase the accuracy of selection and hence the response to selection.

Heritability estimates for both weaning and yearling weight in the present study yielded by Henderson's Method III and REML are similar. Other studies have reported that parameters yielded by Henderson's Method III and REML will be similar if there was no selection operating on the population (Knights *et al.*, 1984, Lin and McAllister, 1984 and Hayes and Cue, 1986). Colleau *et al.* (1989) noted that estimates of genetic parameters and sampling variances provided by Henderson's Method III might be similar to those of REML if the number of progeny per sire was comparatively homogeneous. However, REML is the preferred method if selected populations are to be analysed (Henderson, 1986).

There are positive phenotypic and genetic correlation coefficients between weaning and yearling weight for Bali cattle in the present study. The estimated genetic correlation is larger than the corresponding estimated phenotypic correlation. It indicates that although the observed relationship between weaning and yearling weight is small, a strong positive genetic relationship is found between weaning and yearling weight. Swiger (1961) suggested that many of the same genes are responsible for growth during pre-weaning and post-weaning periods. Results of the present study suggests that selection for weaning weight will result in a positive genetic response in yearling weight in Bali cattle.

Although the phenotypic and genetic correlation coefficients between weaning and yearling weight fall in the range of results from various literatures sources, it appears they are lower than those of other breeds. Environmental variation experienced by an animal during its stage of growth is a possible factor contributing to the low estimated correlations. Compensatory growth of

individuals during post-weaning stage may cause a downward bias of the phenotypic covariance between weaning and yearling traits (Franscoise *et al.*, 1973, Kennedy and Henderson, 1975b). DeNise and Torabi (1989) studied Hereford bulls in a stressful environment and reported that the phenotypic correlation between weaning and yearling weight for good years was higher than for poor years. Animals with the better environment during pre-weaning period were then more affected by the poor post-weaning environment.

Following from results and discussion of the present study, it can be concluded that the low heritability estimates for weaning and yearling weight for Bali cattle suggest that all sources of information (for example, from sibs and progeny) should be included with the sire's own performance in order to increase the accuracy of estimating the sire's genetic merit for these traits. Moreover, the use of Best Linear Unbiased Prediction (BLUP) methodology to estimate breeding values for animals in the Bali beef cattle improvement programme is encouraged to further enhance genetic gain.

Phenotypic and genetic parameters of weaning and yearling weight obtained from the present study can be used to derive a selection index for achieving the selection objective of the Bali cattle improvement program. An increase in carcass weight and maintenance of fat levels could be components of the overall selection objective of Bali beef cattle. To construct a selection index, detailed information such as relative economic values, phenotypic standard deviation, phenotypic correlations and genetic correlations among all economic traits (for example, body weight, carcass weight and carcass composition) of Bali cattle are required. It should be noted that phenotypic and genetic parameters needed for implementing an animal improvement program should be derived from the same breed and environment in which selection is to occur, as they are specific for a particular population. For a long term improvement program of Bali cattle, further studies to examine relative economic values and, phenotypic and genetic parameters of all economic traits of Bali beef cattle are required.

APPENDICES

APPENDIX 1

Appendix 1.1: Distribution of progeny per sire (nested within village) for weaning and yearling weight [1,2].

No. Village	No.	Sire identity	Number of progeny		
			Weaning	Yearling	Weaning and yearling
1. Biaung					
	1).	180	54	51	39
	2).	279	115	109	84
	3).	378	41	39	31
	4).	381	62	48	44
	5).	478	52	50	36
	6).	482	24	17	17
	7).	981	30	29	25
	8).	1080	7	5	5
2. Babahan					
	9).	578	62	42	34
	10).	678	39	30	25
3. Rianggede					
	11).	781	99	86	85
	12).	881	24	21	21
4. Mangeste					
	13).	1182	84	79	78
	14).	1283	7	8	6
	15).	1483	33	24	23
5. Penebel					
	16).	1883	85	74	74
6. Petiga					
	17).	5279	80	51	42
	18).	5380	42	14	13
	19).	5478	42	25	23
	20).	5481	5	*	*
	21).	5581	22	*	*
7. Tuwa	22).	5678	75	72	63
	23).	5681	32	11	11
	24).	5780	40	38	29
	25).	7585	17	4	4
8. Selanbawak					
	26).	5878	2	*	*
	27).	5880	32	31	28
	28).	5882	5	*	*
	29).	5978	42	37	33

appendix 1.1 (continued)

	30).	5981	22	16	16
	31).	6078	9	8	8
	32).	6079	35	26	25
9. Beringkit					
	33).	6178	38	27	26
	34).	6181	11	6	6
10. Batanyuh					
	35).	6281	100	85	83
	36).	6381	51	49	45
	37).	6383	28	15	14
11. Tegaljadi					
	38).	6482	39	27	27
	39).	6483	30	17	17
	40).	6582	61	43	43
12. Kukuh					
	41).	6682	51	40	38
	42).	6782	40	30	27
13. Kuwum					
	43).	6883	15	13	13
	44).	6884	11	*	*
	45).	6984	4	*	*
14. Angsri					
	46).	10179	86	62	54
	47).	10279	72	61	52
	48).	10282	4	*	*
	49).	10379	31	29	23
	50).	10380	31	20	16
	51).	10479	40	39	31
	52).	10480	9	3	3
	53).	10481	13	3	3
15. Senganan					
	54).	10579	26	26	22
	55).	10581	36	18	17
	56).	10583	7	8	7
	57).	10679	104	69	63
	58).	10682	23	22	21
	59).	10779	70	48	42
	60).	10782	34	18	17
	61).	10879	66	54	49
	62).	10881	78	65	59
	63).	10883	20	13	12
	64).	11482	55	52	49
	65).	11485	3	*	*
16. Apuan					
	66).	10979	45	33	25
	67).	10982	4	*	*
	68).	11079	38	30	29
	69).	11080	37	28	24
	70).	11179	80	62	48
	71).	11182	16	6	5

appendix 1.1 (continued)

appendix 1.1 (continued)

17. Luwus

72).	11279	38	32	29
73).	11281	14	10	9

18. Gadungan

74).	15280	35	32	27
75).	15282	19	18	17
76).	15380	77	74	70
77).	15480	64	63	54
78).	15481	25	20	19
79).	15483	3	3	3
80).	15582	16	16	16

19. Selemadeg

81).	15680	30	31	25
82).	15681	49	35	30
83).	15780	44	35	30

20. Mambang

84).	15880	35	33	31
85).	15881	36	27	22
86).	15883	3	3	3
87).	16782	5	4	4

21. Berembeng

88).	15980	31	36	27
89).	15982	7	*	*

22. Tangguntitih

90).	16081	47	41	32
91).	16181	39	37	29
92).	16182	2	*	*
93).	16281	18	15	13

23. Timpag

94).	16381	54	40	39
95).	16382	48	31	30
96).	16682	90	75	75

24. Kesiut

97).	16481	136	107	107
98).	16582	11	6	6

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[1] : * = no records are available.

[2] : summary :

Weaning weight		Yearling weight		Weaning and yearling weight	
Village	: 24	Village	: 24	Village	: 24
Sire	: 98	Sire	: 87	Sire	: 87
Progeny	: 3803	Progeny	: 2990	Progeny	: 2679

Fig. 1: Calving pattern of Bali cattle for 2 year old cows
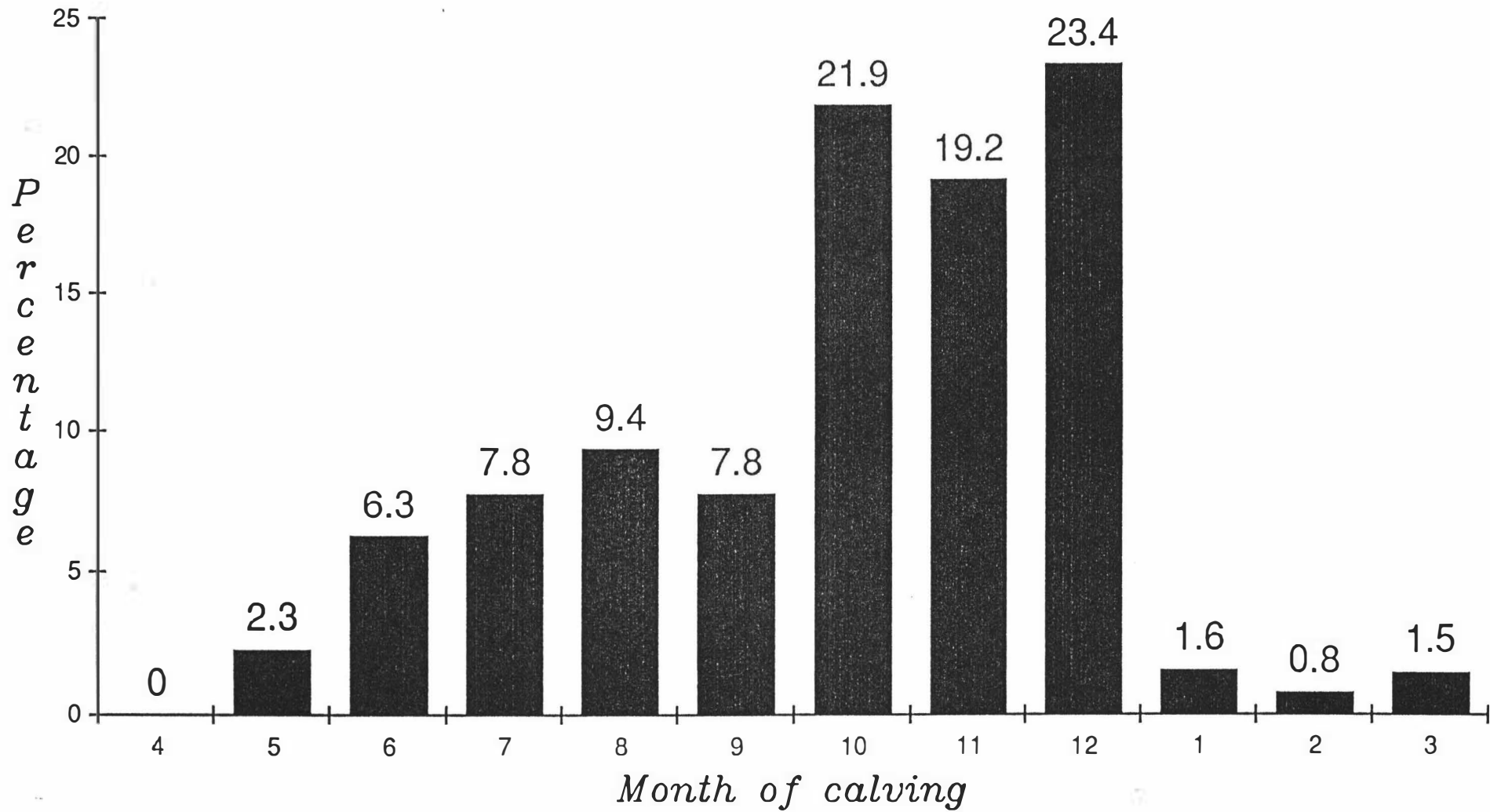
Fig. 2: Calving pattern of Bali cattle for 3 year old cows
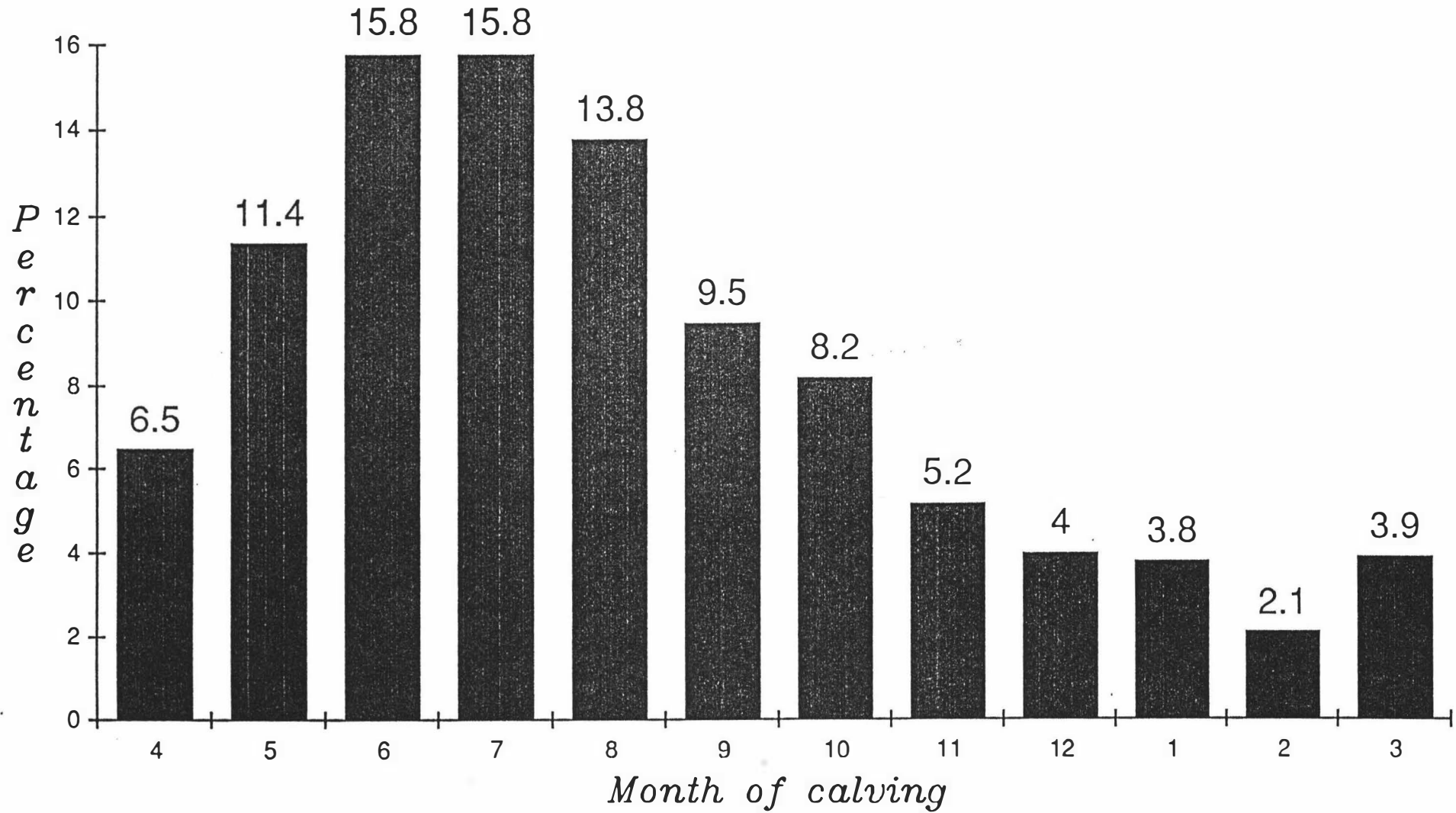
Fig.3: Calving pattern of Bali cattle for >3 year old cows
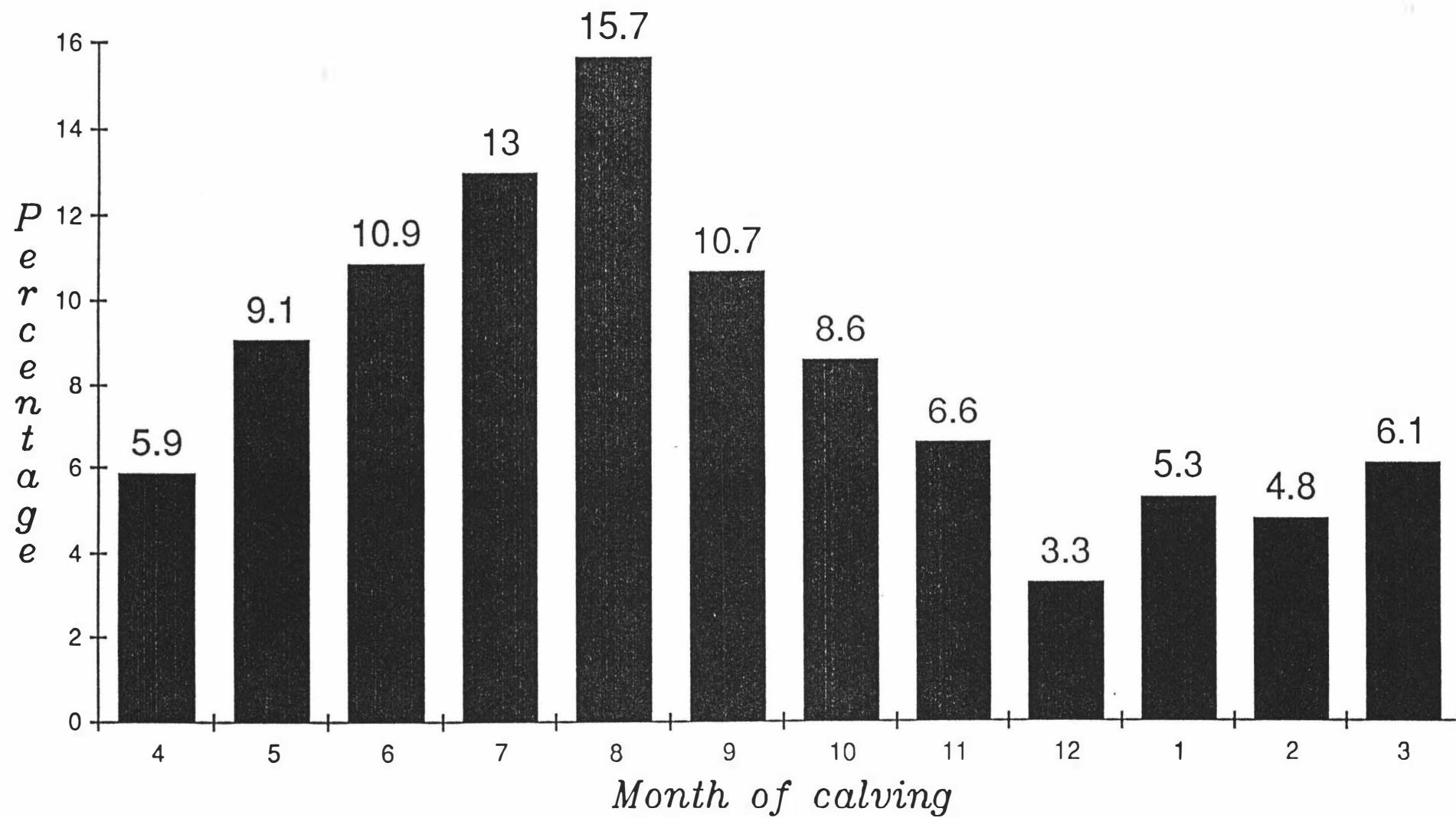
Fig. 4: Calving pattern of Bali cattle (1983–1987)
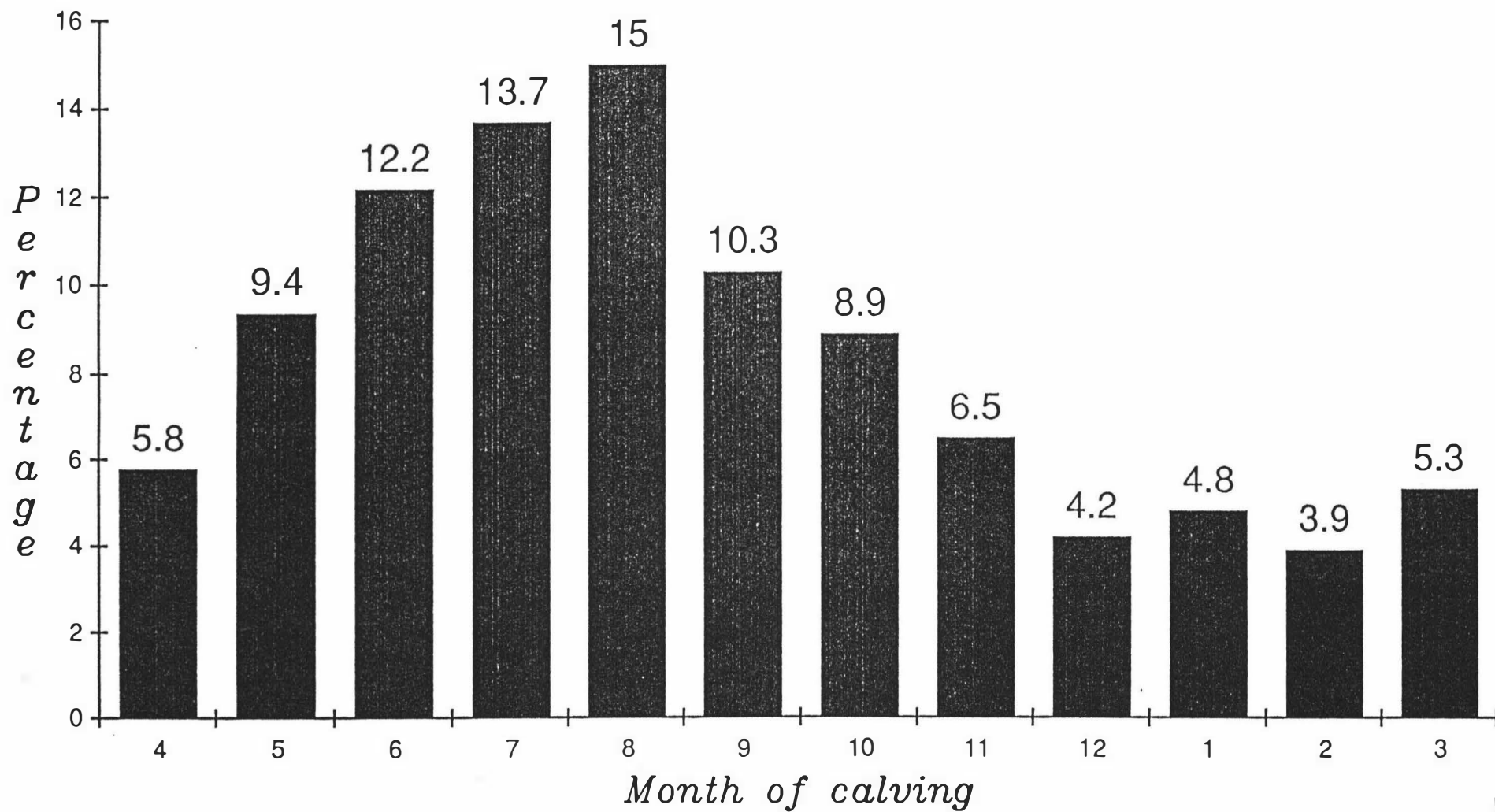
APPENDIX 3

<u>Appendix 3.1:</u> Equation for model 1 for clarifying the non-genetic main effect of village, year of birth, season of birth, dam age group and sex of calf with 24, 5, 2, 6 and 2 subclasses respectively, and age at weighing as a covariate on weaning and yearling weight.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + bX + e_{ijklm}$$

where :

Y_c : the record on weaning and yearling weight,

μ : the general mean,

A_i : the effect of ith village (i = 1, 2, ..., 24),

B_j : the effect of jth year of birth (k = 1, 2, ..., 5 where 1 = 1983, 2 = 1984, 3 = 1985, 4 =1986 and 5 = 1987),

C_k : the effect of kth season of birth (k = 1, 2 where 1 = dry season and 2 = wet season),

D_l : the effect of lth age group of dam (l = 1, 2, ..., 6 where 1 = 2 years, 2 = 3 years, 3 = 4 years, 4 = 5 years, 5 = 6 years and 6 = 7 years),

E_m : the effect of mth sex of calf (m = 1 and 2, where 1 = heifer and 2 = bull),

X   : the age of animals at weighing,

b   : coefficient regression of Y_c on X, and

e_{ijklm} : the common residual which is assumed to have a normal distribution, zero mean and common variance.

Appendix 3.2: Equation for model 2 for clarifying the non-genetic main effect of village, year of birth, season of birth, dam age group and sex of calf with 24, 5, 2, 3 and 2 subclasses respectively, and age at weighing as a covariate on weaning and yearling weight.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + bX + e_{ijklm}$$

where all symbols and assumptions are as in model 1, except $l = 1, 2, 3$ where $1 = 2$ years, $2 = 3$ years and $3 = 4, 5, 6$ and 7 years.

Appendix 3.3: Equation for model 3 for clarifying the non-genetic main effect of village, year of birth, season of birth, dam age group and sex of calf with subclasses as in model 2, all first order interactions among main effects and age at weighing as a covariate on weaning and yearling weight.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + AB_{ij} + AC_{ik} + AD_{il} + AE_{im} + BC_{jk} + BD_{jl} + BE_{jm} + CD_{kl} + CE_{km} + DE_{lm} + bX + e_{ijklm}$$

where :

AB_{ij}, AC_{ik}, AD_{il} and AE_{im} is the interaction between village and year of birth, season of birth, dam age group and sex of calf, respectively,

BC_{jk}, BD_{jl} and BE_{jm} is the interaction between year of birth and season of birth, dam age group and sex of calf, respectively,

CD_{kl} and CE_{km} is the interaction between season of birth and dam age group and sex of calf, respectively,

DE_{lm} is the interaction between dam age group and sex of calf, and

other symbols and assumption are as in the model 1.

Appendix 3.4: Equation for model 4 for clarifying model analysis of weaning weight by fitting the non-genetic main effects as in the model 2, age at weighing as a covariate and all first order significant interactions among main effects according to results of model 3.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + AB_{ij} + AC_{ik} + BC_{jk} + BE_{jm} + CD_{kl} + DE_{lm} + bX + e_{ijklm}$$

where all symbols and assumptions are as in model 1 and model 3.

Appendix 3.5: Equation for model 5 for clarifying model analysis of yearling weight by fitting the non-genetic main effects as in the model 2, age at weighing as a covariate and all first order significant interactions among main effects according to results of model 3.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + AB_{ij} + AC_{ik} + AD_{il} + AE_{im} + BE_{jm} + CD_{kl} + DE_{lm} + bX + e_{ijklm}$$

where all symbols and assumptions are as in model 1 and model 3.

Appendix 3.6: Equation for model 6 by fitting all non-genetic main effects and their significant interactions on weaning weight according to results of model 3 as fixed effects and sires nested within village as random effects

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + AB_{ij} + AC_{ik} + BC_{jk} + BE_{jm} + CD_{kl} + DE_{lm} + bX + S_{n(i)} + e_{ijklm}$$

where :

$S_{n(i)}$: the random effect of the nth sire nested in the ith village, and

other symbols are as in model 1 and model 3.

It was assumed that $S_{n(i)}$ and e_{ijklm} were to be uncorrelated variables with zero means.

Appendix 3.7: Equation for model 7 by fitting all non-genetic main effects and their significant interactions on yearling weight according to results of model 3 as fixed effects and sires nested within village as random effects.

$$Y_c = \mu + A_i + B_j + C_k + D_l + E_m + AB_{ij} + AC_{ik} + AD_{il} +$$
$$AE_{im} + BE_{jm} + CD_{kl} + DE_{lm} + bX + S_{n(i)} + e_{ijklm}$$

where :

all symbols are as in model 1 and model 3 and assumptions are as in model 6.

APPENDIX 4

Appendix 4.1: Analysis of variance of weaning weight and yearling weight using model 1 and the percentage of variation controlled (%VC) by each non-genetic effect (6 dam age classes) [1,2].

Source of variation	Df	Weaning Weight Mean Squares	Sign.	%VC	Df	Yearling weight Mean Squares	Sign.	%VC
Village	23	1714.29	**	2.81	23	9658.27	**	14.75
Year of birth	4	31525.55	**	8.99	4	4455.08	**	1.18
Season of birth	1	75.77	NS	0.01	1	2876.57	**	0.19
Dam age group	5	140.92	NS	0.05	5	4777.87	**	1.58
Sex of the calf	1	83253.82	**	5.93	1	152370.18	**	10.12
Age (covariate)	1	46908.39	**	46.12	1	392112.18	**	26.04
Error	3766	134.43		36	2954	235.06		46

[1] : Df = degree of freedom, VC = variation controlled, Sign = significance, NS =non-significant, * = significant (P < .05) and ** = highly significant (P < .01).

[2] : Total sum of squares (weaning weight) = 1402769.56
R-Square (weaning weight) = 64%
Total sum of squares (yearling weight) = 1505589.12
R-Square (yearling weight) = 54%

Appendix 4.2: Analysis of variance of weaning weight and yearling weight using model 1 and the percentage of variation controlled (%VC) by each non-genetic effect (3 dam age classes) [1,2].

Source of variation	Df	Weaning Weight Mean Squares	Sign.	%VC	Df	Yearling weight Mean Squares	Sign.	% VC
Village	23	1714.29	**	2.81	23	9658.27	**	14.75
Year of birth	4	31525.56	**	8.99	4	4455.08	**	01.18
Season of birth	1	75.78	NS	0.01	1	2876.57	**	00.19
Dam age group	2	1.51	NS	0.00	2	9758.03	**	01.29
Sex of the calf	1	83166.23	**	5.93	1	154217.75	**	10.24
Age (covariate)	1	646920.45	**	46.12	1	394346.27	**	26.19
Error	3769	134.54		36	2957	234.92		46

[1] : All abbreviations as in appendix 4.1 .

[2] : Total sum of squares (weaning weight) = 1402769.57 and R-Square (weaning weight) = 64%

Total sum of squares (yearling weight) = 1505589.12 and R-Square (yearling weight) = 54%

Appendix 4.3: Analysis of variance of weaning weight using model 3 and the percentage of variation controlled (%VC) by each non-genetic effect [1,2].

Source of variation	Df	Mean Squares	Sign.	%VC
Village	23	1714.29	**	2.81
Year of birth	4	31525.56	**	2.81
Season of birth	1	75.78	NS	0.01
Dam age group	2	1.51	NS	0.00
Sex of the calf	1	83166.23	**	5.93
Village by year	52	989.75	**	3.67
Village by season	23	1303.53	**	2.14
Village by dam age	35	567.81	**	1.42
Village by sex	23	549.79	**	0.90
Year by season	4	3165.74	**	0.90
Year by dam age	7	329.32	*	0.16
Year by sex	4	2129.74	**	0.61
Season by dam age	2	293.03	NS	0.04
Season by sex	1	28.90	NS	0.00
Dam age by sex	2	1157.07	**	0.17
Age (covariate)	1	565205.60	**	40.29
Error	3616	124.01		32

[1]   :   All abbreviation as in appendix 4.1 .

[2]   :   Total sum of squares = 1402769.57
        R-Square (weaning weight) = 68%

Appendix 4.4: Analysis of variance of yearling weight using model 3 and the percentage of variation controlled (%VC) by each non-genetic effect [1,2].

Source of variation	Df	Mean Squares	Sign.	%VC
Village	23	9658.28	**	14.75
Year of birth	4	4455.08	**	01.18
Season of birth	1	2876.57	**	00.19
Dam age group	2	9758.03	**	01.29
Sex of the calf	1	154217.75	**	10.24
Village by year	46	2687.45	**	08.21
Village by season	23	1390.95	**	02.12
Village by dam age	36	425.37	**	01.01
Village by sex	23	741.29	**	01.13
Year by season	4	1204.37	**	00.31
Year by dam age	6	565.98	*	00.22
Year by sex	4	1872.60	**	00.49
Season by dam age	2	220.55	NS	00.02
Season by sex	1	121.35	NS	00.00
Dam age by sex	2	806.19	*	00.10
Age (covariate)	1	306931.21	**	20.38
Error	2810	205.06		38

[1] : All abbreviation as in appendix 4.1

[2] : Total sum of squares = 1505589.12

R-Square (yearling weight) = 62%

Appendix 4.5: Analysis of variance of weaning weight using model 4 and the percentage of variation controlled (%VC) by each non-genetic effect [1,2].

Source of variation	Df	Mean Squares	Sign	%VC
Village	23	1714.29	**	2.81
Year of birth	4	31525.56	**	8.99
Season of birth	1	75.78	NS	0.01
Dam age group	2	1.51	NS	0.00
Sex of the calf	1	83166.23	**	5.93
Village by year	52	989.75	**	3.67
Village by season	23	1303.53	**	2.14
Year by season	4	3620.89	**	1.03
Year by sex	4	2798.74	**	0.79
Season by dam age	2	657.98	**	0.09
Dam age by sex	2	490.72	*	0.07
Age (covariate)	1	586125.79	**	41.78
Error	3682	124.51		33

[1] : All abbreviation as in appendix 4.1

[2] : Total sum of squares = 1402769.57

R-Square = 67%

Appendix 4.6: Analysis of variance of yearling weight by using model 5 and the percentage of variation controlled (%VC) by each non-genetic effect [1, 2].

Source of variation	Df	Mean Squares	Sign	%VC
Village	23	9658.27	**	14.75
Year of birth	4	4455.08	**	1.18
Season of birth	1	2876.57	**	1.18
Dam age group	2	9758.03	**	1.29
Sex of the calf	1	154217.75	**	10.24
Village by year	46	2687.45	**	8.21
Village by season	23	1390.94	**	2.12
Village by dam age	36	425.36	**	1.01
Village by sex	23	741.29	**	1.13
Year by sex	4	1774.83	**	0.47
Season by dam age	2	68.64	*	0.00
Dam age by sex	2	912.70	**	0.12
Age (covariate)	1	313507.53	**	20.82
Error	2821	205.05		38

[1]   : All abbreviation as in appendix 4.1

[2]   : Total sum of squares = 1505589.12

       R-Square = 62%

<u>Appendix 4.7:</u> Analysis of variance of weaning weight using model 6 and the percentage of variation controlled (%VC) by each effect [1,2].

Source of variation	Df	Mean Squares	Sign	%VC
Village	23	1714.29	**	2.81
Year of birth	4	31525.56	**	8.99
Season of birth	1	75.78	NS	0.01
Dam age group	2	1.51	NS	0.00
Sex of the calf	1	83166.23	**	5.93
Village by year	52	989.75	**	0.10
Village by season	23	1303.53	**	2.14
Year by season	4	3620.89	**	1.03
Year by sex	4	2798.74	**	0.79
Season by dam age	2	657.98	**	0.09
Dam age by sex	2	490.72	*	0.07
Age (covariate)	1	586125.78	**	41.78
Sire (village)	70	237.19	**	1.18
Error	3612	122.32		32

[1] : All abbreviation as in appendix 4.1
[2] : Total sum of squares = 1402769.56
R-Square = 68%

Appendix 4.8: Analysis of variance of yearling weight using model 7 and the percentage of variation controlled (% VC) by each effect [1,2].

Source of variation	Df	Mean Squares	Sign	%VC
Village	23	9658.27	**	14.75
Year of birth	4	4455.08	**	1.18
Season of birth	1	2876.57	**	0.19
Dam age group	2	9758.03	**	1.29
Sex of the calf	1	154217.75	**	10.24
Village by year	46	2687.45	**	8.21
Village by season	23	1390.94	**	2.12
Village by dam age	36	425.36	**	1.01
Village by sex	23	741.29	**	1.13
Year by sex	4	1774.83	**	0.47
Season by dam age	2	68.64	**	0.01
Dam age by sex	2	912.70	*	0.12
Age (covariate)	1	313507.53	**	20.82
Sire (village)	59	408.49	**	1.60
Error	2762	200.71		37

[1] : All symbols and abbreviations as in appendix 4.1

[2] : Total sum of squares = 1505589.12

R-Square = 63%

<u>Appendix 4.9:</u> Analysis of variance of weaning weight and yearling weight of records for deriving correlation coefficients between weaning and yearling weight [1,2].

Source of variation	Df	Weaning weight Mean Squares	Sign	Yearling weight Mean Squares	Sign
Village	23	1958.22	**	7100.31	**
Year	4	19283.02	**	5062.77	**
Season	1	1101.75	**	1135.52	*
Dam age group	2	280.70	NS	8902.76	**
Sex	1	56625.64	**	138211.47	**
Village by year	46	660.03	**	2159.77	**
Year by season	4	912.66	**	2197.36	**
Year by sex	4	2678.88	**	2421.70	**
Season by dam age group	2	354.61	**	181.74	NS
Dam age group by sex	2	239.85	*	806.13	*
Age (covariate)	1	387473.38	**	257745.61	**
Sire (village) 59		171.27	**	346.70	**
Error	2529	115.01		206.88	
R-Square		0.68		0.59	

[1] : All abbreviations are as in appendix 4.1.

[2] : Sum of weaning and yearling weight :

Sire (village) :

Degree of freedom   =   59

Mean sum of squares   =   727.61

Error :

Degree of freedom   =   2528

Mean sum of squares   =   417.13

APPENDIX 5

<u>Appendix 5.1</u> :   Number of animals, Least squares means (LSM) and standard error (SE) of weaning and yearling weight for each non-genetic effect.

Classes / subclasses (non-genetic effects)	Weaning Weight			Yearling weight		
	No. of animals	LSM	SE	No. of animals	LSM	SE
Village						
Angsri	286	86.00	0.91	217	135.53	1.42
Apuan	219	83.48	0.95	159	136.02	1.49
Babahan	101	84.95	1.31	72	149.25	2.05
Biaung	385	89.65	0.73	348	153.83	1.07
Brembeng	38	81.69	1.95	36	127.32	2.69
Beringkit	49	81.72	1.76	33	135.30	2.83
Batanyuh	179	85.42	0.95	149	141.58	1.38
Gadungan	239	80.69	0.89	226	130.16	1.26
Kukuh	91	84.65	1.29	70	142.65	1.94
Kesiut	147	85.97	1.04	113	139.48	1.57
Kuwum	30	88.04	2.18	13	145.71	4.33
Luwuh	52	87.47	1.73	42	141.72	2.56
Mambang	79	82.92	1.39	67	132.23	2.01
Mangeste	124	87.06	1.16	111	134.57	1.63
Petiga	191	84.79	1.02	90	138.30	1.90
Penebel	85	87.69	1.37	74	137.17	1.97
Riang-gede	123	94.37	1.08	107	145.05	1.54
Selanbawak	147	86.62	1.11	118	141.14	1.69
Selanmadek	123	79.71	1.15	101	126.24	1.70
Senganan	522	85.73	0.65	393	136.63	0.98
Tangguntitih	106	79.37	1.18	93	124.14	1.70
Tegaljadi	130	84.38	1.10	87	142.72	1.76
Timpag	192	84.70	0.93	146	141.22	1.40
Tuwah	164	87.23	1.02	125	137.99	1.61
Year of birth						
1983	1201	88.62	0.51	1127	135.90	0.74
1984	1049	86.40	0.56	707	134.78	0.86

appendix 5.1 (continued)

1985	666	84.97	0.64	434	147.09	1.03
1986	496	88.33	0.74	487	137.55	1.07
1987	390	77.56	0.82	235	135.50	1.38
Season of birth						
Dry season	2523	85.35	0.48	2057	138.07	0.74
Wet season	1279	85.01	0.51	933	138.25	0.80
Dam age group						
2-year olds	128	83.95	1.16	108	140.38	1.72
3-year olds	1068	85.44	0.43	897	134.69	0.68
>3-year olds	2606	86.14	0.30	1985	139.42	0.48
4-year olds	1191	86.33	0.40	974	139.59	0.62
5 year olds	920	86.44	0.44	669	139.29	0.70
6 year olds	971	84.91	0.61	290	139.48	1.02
7-year olds	74	86.90	1.41	52	137.08	2.27
Sex of the calf						
Bull	1966	89.82	0.49	1564	145.47	0.75
Heifer	1836	80.54	0.49	1426	130.86	0.75

APPENDIX 6

Appendix 6.1: Procedures for calculation of the additive genetic variance, a heritability estimate and standard error by Henderson's Method III based on SAS ANOVA (a case for weaning weight).

1. **Formulae**

$$E\,[MS_{(s:v)}] = \sigma^2_e + k\,\sigma^2_s \quad\text{...}\quad (6.1.1)$$

$$k = [\,1/(s-v)\,]\,[\,n_{...} - \Sigma_i\,\{\,(\Sigma_j n_{ij}^2.)/n_{i..}\,\}\,] \quad\text{.....................................}\quad (6.1.2)$$

$$\hat{h}^2 = [\,(4)(\hat{\sigma}^2_s)\,]/[\,\hat{\sigma}^2_s + \hat{\sigma}^2_e\,]. \quad\text{...}\quad (6.1.3)$$

$$SE_{(\hat{h}^2)} = 4\,(\,2\,[\,\{n_{...}-1\}\{1-.25h^2)^2\}]\,[\,\{1+(k-1)\,.25h^2\}^2\,/\,[\,k^2(n_{...}-s)(s-1)\,]\,)^{0.5}$$

where :

$E\,[MS_{(s:v)}]$	:	the expectation of the mean square of sire nested within village,
$\hat{\sigma}^2_e$	:	the within sire variance component (the error variance component),
$\hat{\sigma}^2_s$	:	the between sire within village variance component,
k	:	coefficient of between sire variance component,
$s-v$	:	degree of freedom of sire nested within village,
$n_{...}$	:	total number of progeny,
$n_{ij}^2.$	:	square of number of progeny of the jth sire nested in the ith, village,
$n_{i..}$	:	total progeny in the ith village,
h^2	:	heritability estimate, and
SE	:	standard error.

2. **Required information**
    1. $\hat{\sigma}^2_e$ = 122.32 (appendix 4.7)
    2. $MS_{(s:v)}$ = 237.19 (appendix 4.7)
    3. $s-v$ = 70 (appendix 4.7)
    4. $n_{...}$ = 3803 (appendix 1.1)
    5. $\Sigma_i\,\{\,(\Sigma_j nij^2.)/n_{i..}\,\} = 1299$ (deriving from appendix 1.1)

3. **Calculation**
    1. $k = [\,1/(s-v)\,]\,[\,n_{...} - \Sigma\,\{nij^2./n_{i..}\}\,]$
       Substitute all available information
       $k = 35.7$
    2. $E\,[MS_{(s:v)}] = \sigma^2_e + k\,\sigma^2_s$
       Substitute all available information
       $\hat{\sigma}^2_s = 3.22$
    3. $h^2 = [\,(4)(\sigma^2_s)\,]/[\,\sigma^2_s + \sigma^2_e\,].$
       Substitute all available information
       $\hat{h}^2 = 0.11$
    4. $SE_{h^2} = 4\,(\,2\,[\,\{n_{...}-1\}\{1-.25h^2)^2\}]\,[\,\{1+(k-1)\,.25h^2\}^2\,/\,[\,k^2(n_{...}-s)(s-1)\,]\,)^{0.5}$
       Substitute all given information
       $SE_{\hat{h}^2} = 0.03$

Appendix 6.2: Procedures for calculation the genetic correlation between weaning and yearling weight based on variance components yielded by Henderson's Method III (Becker, 1984).

1. Formulae

$$\hat{\sigma}_{S(ww,yw)} = [\hat{\sigma}^2_{S(ww+yw)} - \hat{\sigma}^2_{S(ww)} - \hat{\sigma}^2_{S(yw)}] / 2 \quad .... (6.2.1)$$

$$\hat{\sigma}_{E(ww,yw)} = [\hat{\sigma}^2_{E(ww+yw)} - \hat{\sigma}^2_{E(ww)} - \hat{\sigma}^2_{E(yw)}] / 2 \quad .... (6.2.2)$$

$$\hat{r}_g = [\hat{\sigma}_{S(ww,yw)}] / [\{\hat{\sigma}^2_{S(ww)}\}\{\hat{\sigma}^2_{S(yw)}\}]^{0.5} \quad .... (6.2.3)$$

where :

$\hat{\sigma}^2_{S(ww)}$: sire variance component of weaning weight,

$\hat{\sigma}^2_{E(ww)}$: residual variance of weaning weight,

$\hat{\sigma}^2_{S(yw)}$: sire variance component of yearling weight,

$\hat{\sigma}^2_{E(yw)}$: residual variance of yearling weight,

$\hat{\sigma}_{S(ww,yw)}$: genetic covariance between weaning and yearling weight,

$\hat{\sigma}_{E(ww,yw)}$: environmental covariance between weaning and yearling weight,

$\hat{\sigma}^2_{S(ww+yw)}$: sire variance of total of weaning and yearling weight

$\hat{\sigma}^2_{E(ww+yw)}$: environmental variance of total of weaning and yearling weight, and

$\hat{r}_g$: genetic correlation coefficient between weaning and yearling weight.

2. Required information

a) Weaning weight :

$\hat{\sigma}^2_{E(ww)}$ = 115.01 (appendix 4.9)

$\hat{\sigma}^2_{S(ww)}$ = 1.98 (derived from appendix 1.1 and appendix 4.9)

b) Yearling weight :

$\hat{\sigma}^2_{E(yw)}$ = 206.88 (appendix 4.9)

$\hat{\sigma}^2_{S(yw)}$ = 4.91 (derived from appendix 1.1 and appendix 4.9)

c) [weaning + yearling weight] :

$\hat{\sigma}^2_{E(ww+yw)}$ = 417.13 (from appendix 4.9)

$\hat{\sigma}^2_{S(ww+yw)}$ = 10.90 (deriving from appendix 1.1. and 4.9)

3. Calculations

Covariance components

Substitute all available information into formulae 6.2.1 and 6.2.2, so :

$\hat{\sigma}_{E(ww,yw)}$ = 47.62

$\hat{\sigma}_{S(ww,yw)}$ = 2.01

The genetic correlation :

Substitute all available information into formulae 6.2.3, so :

$\hat{r}_g$ = .64

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