# DEVELOPING BREEDING OBJECTIVES FOR THE NGUNI CATTLE BREED IN SOUTH AFRICA

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# DECLARATION

I declare that the thesis hereby submitted to the University of Limpopo for the degree of Doctor of Philosophy (Animal Breeding) has not previously been submitted by me for a degree at this or any other university, that it is my own work in design and execution, and that all material contained therein has been duly acknowledged.

Matjuda Lehotlo E [redacted]

Date

# DEDICATION

This work is dedicated to my mom, my first teacher of “animal production”, Edith Motlatšo Matjuda, and my late dad Matladi Victor Matjuda

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# ABSTRACT

Direction in which a breed should be developed is determined by definition of breeding objectives for various stakeholders. However, breeding objectives have not been determined for the indigenous Nguni breed; particularly with reference to emerging and subsistence cattle owners. The objectives were to: 1) describe demographic structure of the Nguni breed based on historical data submitted to the National Beef Cattle Improvement Scheme; 2) develop an index-in-retrospect to assess selection applied by Nguni breeders, and determine whether the recorded historical data from the Nguni breed show no genetic trend for performance measures and thus are consistent with the subsistence phase of production; and 3) develop forward-looking breeding objectives reflective of the production, profitability, and sustainable phases of production. Data from the Nguni herdbook was used to compile: 1) the numbers of offspring recorded each year and their parents; 2) the number and proportion of the recorded sires and dams that produced progeny that subsequently became parents; 3) age distribution of South African Nguni males in reproduction by year of birth of their offspring, 4) age distribution of South African Nguni females in reproduction by year of birth of their offspring, and 5) distribution of females by parity number. The genetic make-up of the recorded Nguni population was further summarized by: 1) generation number relative to the first recorded ancestor and generation interval, 2) distribution of family size, and 3) inbreeding coefficient relative to first recorded ancestor**.** For population growth projections the model of Leslie was used. The estimated breeding values from the South African Nguni national genetic evaluation were used to calculate the genetic selection differentials and an index-in-retrospect. Simulation was used to determine breeding objectives for the Nguni breed throughout four phases of production viz pioneering/subsistence, production, productivity and sustainability. Parameters of the simulation were, to the extent possible, consistent with phenotypic data gathered in the South African national system for genetic evaluation and previous research. Demographic and genetic analyses indicate the generation intervals were 5.7 and 5.9 years for sires and dams, respectively. Effective population size of Nguni was estimated to be 168. Opportunity exists to increase the rate of genetic improvement by shortening the selection paths from sire to descendants. Reducing age of first calving to two years would increase numbers of females in reproduction and calves produced per year. Through 2006, there had been little or no selection applied to recorded performance measures, resulting in very small amounts of genetic trend. Also compromising any potential for response to selection was a lack of consistency in selection applied to males and females. For males, selection by breeders was largely consistent with natural selection. However, the imposed and natural selection of females was less consistent. In the breeding objectives, emphasis placed on growth traits tended to diminish and emphasis placed on female survival increased with progression through the phases of production. However, the breeding objectives were highly correlated and would be expected to move the breed in the same general direction. Therefore producers, irrespective of where they viewed themselves as being positioned relative to the three phases of production, could contribute to the breeding of Nguni cattle. Incorporation of these breeding objectives in the national cattle evaluation system may enhance their use by farmers. These results can help subsistence and emerging farmers increase the production of their herds with resulting greater profitability.

# CHAPTER 1

# GENERAL INTRODUCTION

## *1.1 Background*

The genetic standard of a breed universally depends on the breeding strategy of an elite group of breeders that sit at the top of the breeding pyramid (Lush, 1946). The second group from the top of the breeding pyramid, who are the multipliers, can be identified as that group which buys genetic materials from the elite group and sells progenies to commercial farmers. Generally, emerging and subsistence cattle owners derive their genetic material from multipliers and commercial farmers (MacNeil and Matjuda, 2007). In this approach, gene flow is unidirectional, normally from the elite top group to the farmer at the bottom of the breeding pyramid (English *et al*., 1996). The flow of genes from the elite breeders downward to farmers lower in the pyramid suggests that selection decisions made by the few determine the breeding progress made by the entire class of primary producers. Primary producers are, for the purposes of the study, the cattle farmers whose end products are animals destined to secondary producers such as feedlots. Thus, genetic change in beef cattle production appears to be a function of the decisions of the elite group of breeders.

Bawden (1989) described four phases in the evolution of production systems: pioneering, production, productivity, and persistency. Here, the pioneering phase is viewed as consistent with ***subsistence*** agriculture in which selection is not practiced in an organized way and thus no genetic trend is expected. The ***production*** phase is viewed as a period of attempted maximization of output. During the productivity phase attention is turned from maximum output to maximizing ***profitability*** or return on investment. Finally, the persistency phase is viewed as being consistent with ***sustainable*** production systems in which resource use is constrained. The phase seeks to maximise the effectiveness and efficiency of resources.

Conceptually, sustainability can be defined in many ways; not all of which can be readily included in quantitative breeding objectives. However, an important aspect of the concept is that the environmental, genetic diversity, ethical and social aspects should be accounted for in addition to short- and long-term economic value (Olesen *et al*., 2000). The underpinning idea of sustainable agricultural approach is that future generations should have, at least as many options as are currently available to explore alternative solutions to food challenges. The common elements of sustainability may include (Olesen *et al.,* 2000):

- *Resource efficiency*: efficient use of non-renewable resources that must be imported in to the farm.
- *Production efficiency*: efficient conversion of renewable resources into products.
- *Economic profitability*: short- and long-run production of value equal or greater than cost.
- *Environmental soundness*: enhanced or improved environment both on the farm and beyond the farm’s borders.
- *Social viability*: equitable social environment that favours owner/operator remaining on the farm.

Groen (2000) provided a detailed discussion on various principles of sustainability in livestock production, which are briefly outlined. In order for a country to achieve sustainability there should be a clear national development objective for agricultural production. In setting a national development objective for agricultural production of livestock, a prerequisite is the compilation of an inventory on land use patterns, animal genetic resources and their local usage, and their strong and weak characteristics. The agricultural production development objective could depend on the development attained by the different typologies in the country. The approach gives direction in optimising the utilisation of the natural resources available. The direction may be formalised in a breeding goal/objective. The breeding objective is a particular combination of breeding values and the economic weighting factors for all the characters in the objective (Hazel, 1943; Falconer and MacKay, 1996; Bourdon, 1997). A breeding objective gives an indication of what “better” and “worse” animals entail, given the total economic production environment. The advantage of a breeding objective is that it can be customised according to the region, farm, breed, breeding group, production system, market and management style and still be congruent to the country’s agricultural development objective, since it is both positive and non-prescriptive.

The dilemma is that all cattle farmers seem to be influenced and encouraged to follow the direction of maximum production or profitability (Olesen *et al.,* 2000). The goal of production per head is based on maximizing income in the short-term, but does not appear to take all elements of sustainable livestock production into consideration. In order to satisfy the aims of production per head basis, costly technological inputs should be provided to mitigate shortcomings of the production environment (Groen, 2000). Generally, provision of technological inputs may be avoided if quantifiable breeding goals are, from the outset, properly formulated and implemented. Further, Van der Westhuizen and Matjuda (1999) hypothesised that the inferred breeding objectives of most elite producers were not congruent with the needs of the primary producers. In the event that the hypothesis holds true, the ability of the cattle breeds to adjust to inconsistent environmental conditions would be negatively affected.

Failure to formulate and implement appropriate quantifiable breeding goals may lead to the production of cattle that are dependent on the owner for economic production, with numerous unintended consequences (Scholtz, 1988). For instance, in South Africa this may lead to cattle competing with humans for cereal grains. In the long-term, feeding cattle with cereal grains may be disadvantageous since it impairs the ability of ruminants to convert grass into scarce protein. Increased uses of chemicals to protect the ill-adapted animals may result in increased assault of non-targets, such as consumers, bees and birds (Scholtz, 1988). Appropriate formulation of the breeding objectives for each stratum in the breeding pyramid could, probably, ameliorate the consequences of inappropriate quantifiable breeding goals (Van der Westhuizen and Matjuda, 1999).

## *1.2 Problem statement*

Compared to exotic cattle breeds, the indigenous Nguni cattle breed is a highly sought-after breed in South Africa, with increased government support in distribution of the germplasm among local farmers. However, the breeding objectives of the Nguni breed have not been determined. The researcher proposes to use simulation to determine the breeding objectives of the Nguni breed throughout the four phases of production defined by Bawden (1989). These computer-based simulations will be constructed at the whole animal level and include, continuous time-dependent processes, events and both stochastic and deterministic elements. Parameters of the simulation will, to the extent possible, be consistent with phenotypic data gathered in the South African national system for genetic evaluation. Model development of breeding objectives for the Nguni cattle breed will build on an existing collaborative research between the Agricultural Research Council (ARC) in South Africa and the United States Department of Agriculture-Agricultural Research Service (USDA-ARS). The development of the proposed Nguni model will enhance the productivity of this highly demanded breed among the emerging and small scale farmers in South Africa.

## *1.2 Motivation of the study*

Development of the breeding objectives for the Nguni cattle breed will help to improve the breed to the level of sustainable production, with increased accessibility to the majority of emerging and small scale farmers in South Africa. Moving toward the formulated breeding objectives is believed to be in line with the agricultural production and development strategies of the Department of Agriculture – Republic of South Africa (2008), which are intended to alleviate poverty.

## *1.3 Aim and objectives of the study*

### *1.4.1* ***Aim***

The aims of the study are to describe the current state of the Nguni population in South Africa and to develop focused breeding objectives for them. The specific objectives of the study will be three-fold:

### *1.4.2* ***Objectives***

The objectives of this study were:

1 To describe demographic structure of the Nguni breed based on historical data submitted to the National Beef Cattle Improvement Scheme.

2 To develop an index-in-retrospect to assess selection applied by Nguni breeders, and determine whether the recorded historical data from the Nguni breed show no genetic trend for performance measures and thus are consistent with the subsistence phase of production.

3 To develop forward-looking breeding objectives reflective of the production, profitability, and sustainable phases of production.

# CHAPTER 2

# LITERATURE REVIEW

## *2.1 Nguni cattle*

Nguni is a hardy cattle breed uniquely adapted to the Southern African environment. The Nguni cattle are a sub-type of the Sanga cattle (*Bos taurus africanis*) (Meyer, 1984). Originally, the name Nguni collectively referred to the Swazi, Zulu and the Landim cattle of Mozambique (Rege and Tawah, 1999). While the origin of the breed is speculative, it has been acknowledged that the breed has been in the ownership of traditional black farmers for centuries (Scholtz and Ramsay, 2007). Thus, the term breed as a formal designation had little meaning and pedigree recording was non-existent (Rege, 2001). The breed is spread throughout the Southern African region and made up of several ecotypes (South African Livestock Breeding, 2004). The current South African context of the term Nguni is as a collective name for a number of ecotypes that are recognised as a distinct group with members sharing particular characteristics. This group is brought together as a breed society to serve the collective interests of the breeders. The most important minimum breed standards are set around fertility measurements *viz* a female's age at first calving should not exceed 39 months with an inter-calving period and interval since last calving not exceeding 730 days.

It is argued that natural selection molded the Nguni into what it is without the interference of man (South African Livestock Breeding, 2004). A more nuanced view is given by Rege (2001): recognizing that in many instances, the local environment, culture and values of communities are reflected in the key traits and/or functions of the livestock "breeds". These may range from such complex traits as adaptation to local environmental stresses, to functions such as traction or products such as beef or milk and simple traits such as presence and size of horns or humps. Behind these traits are the breeding practices and other indigenous knowledge systems that have been applied for the development of ecotypes or segments of the Nguni population and the genetic diversity that they represent.

Ecotypes were largely a result of tribal segregations which are spread throughout the country. The early propagation of diverse Nguni ecotypes was further helped by government policies such as group areas and homelands acts. These policies confined tribes to designated areas with their associated cattle being relatively isolated from those of the other tribes. Cultural practices of different tribes seemingly gave different implied breeding objectives and selection criteria (Rege, 2001). Certain tribes seemingly raised cattle primarily for beef while others engaged primarily in dairying while some valued both products. The environment augmented any imposed selection through natural selection (Tano *et al*., 2003).

For decades, there has been a general perception of the Nguni's inferiority in the South African industrial beef sector. This perception was largely due to lack of documentation on the characteristics of the indigenous livestock during the period of colonization and for an extended period thereafter (Scholtz and Ramsay, 2007). It was probably the result of judging all indigenous livestock on their appearance and on the basis of breeding objectives for a different production system than those in which they were developed (Tano *et al*., 2003; Matjuda, 2005). The perception of inferiority led to the promulgation of an Act in 1934 in which indigenous breeds and types were regarded as 'scrub' or nondescript. Inspectors were appointed to inspect the bulls in communal areas (those in possession of indigenous Africans) and to castrate them if regarded as inferior. Fortunately, this Act was very unpopular and applied effectively for only a few years (Hofmeyr, 1994). The Nguni gene pool was also diluted through crossbreeding with exotic stock.

During the first part of the previous century little or no attention was paid to the potential of indigenous cattle breeds in South Africa, except for the Afrikaner (Scholtz and Ramsay, 2007). However, some commercial farmers in the present KwaZulu-Natal and Swaziland were aware of the value of the breed and used the breed in crossbreeding programs, mainly to counteract the degeneration of local stocks resulting from introduction of exotic breeds in the region (South African Livestock Breeding, 2004). Following the acquisition in 1932 of a number of the nondescript Nguni animals by the late Professor HH Curzon, the Bartlow Combine breeding station was established in 1940. In 1948, a committee under the chairpersonship of Prof. F. N. Bonsma recognized the failure of exotic breeds to perform well under some prevailing environmental conditions. This recognition brought about a formal appreciation of the importance of a harmonious relationship of a breed's hereditary complex with its local environment and recommended that Nguni be recognized as a breed.

The observation that Nguni cattle had, as a result of their environment, evolved into a breed of unusual sturdiness, health and adaptability, was later corroborated by research carried out at the ARC experimental stations and other institutions. The full potential of the Nguni was only demonstrated following the introduction of a beef cattle recording scheme in 1959 and the establishment of the research facility by the then department of Agriculture at Loskop Suid (location) in South Africa and the publication of research results on the Nguni in the early 1980's (Scholtz and Ramsay, 2007).

The realization of the value of the breed generated interest in the Nguni by the commercial farmers and other institutions. This interest ushered in a collection phase and the number of animals recognized as belonging to the Nguni breed steadily increased. In the 1980's, the interest in the Nguni from the commercial sector accelerated and in August 1983 the breed was recognized as a developing breed under the Livestock Improvement Act (No. 25 of 1977) and a breeder's society was established in 1986 (Scholtz and Ramsay, 2007). At that stage, there were about 3,000 Nguni females in a few well managed herds primarily situated on government farms. Most of the governmental breeding stations were established around ecotypes referred to as Zulu, Pedi, Venda, Tshikalanga, and Shangaan cattle (Bothma, 1993; Hamburger and Ramsay, 1984). The Nguni breed, excluding the commercial animals, has now grown to the point of having the second largest number of registered animals recorded on the South Africa's national database (Integrated Registration and Genetic Information System - INTERGIS) on 1 April 2007.

Nguni is currently thought to have positive performance attributes including high fertility, low maintenance requirements, ease of calving, adaptability, resistance to parasites, resistance to tick borne diseases, good temperament, longevity, browsing and good walking ability (Scholtz, 1988; South African Livestock Breeding, 2004). Consequently, the breed is viewed as having cost-effective beef production capacity and the capability to survive under harsh conditions with limited food and water giving it potential for use as a dam line. Nguni is small to medium in size with cows weighing up to about 396kg and bulls weighing up to 900kg (Scholtz, 1988). Recent recognition of its adaptive traits led to its popularity in the commercial/stud breeding sector (Bester *et al*., 2003). The establishment of a breed society in conjunction with newly recognized interest by the government has led to a pronounced supra-regional propagation of the Nguni breed. There are now several projects in place, supported by government, reintroducing the breed into communities and the small scale farming sector (Bester *et al*., 2003).

Ndumu *et al*. (2008) categorizes cattle traits into body, performance and beauty attributes. Beauty traits include horn length, horn orientation, horn angle and colour patterns. The colour pattern of the Nguni varies widely, the frequent pattern involves white hair with pigmented skin, black, brown red, dun, yellow are common, either as solid colours or various combinations, black, tan or bridle (Rege and Tawah, 1999). Some current stud breeders of the Nguni cattle continue to value the colour pattern and argue that the beauty and uniqueness of the breed lies in the colour and the shape of the horns.

Based on claimed environmental adaptation and beauty attributes referenced above, some Nguni stud breeders tend to be skeptical of whether selection for performance would bring about unexpected responses in traits that were not selection criteria as hypothesized by Koch *et al*., (1974). Expressed concerns were that selection for certain traits e,g. weaning weight and post-weaning growth rate might produce undesired correlated responses including increased mature weight, and decreased adaptation and fertility as suggested by Barlow (1978) and Scholtz and Roux (1984).

Nguni is the second biggest breed recorded in the national database. However, only about 27% of breeders are taking part in the national performance testing scheme. Part of the problem of low participation is that traditional breeders, who originally bred the animals, did not keep any documentation of those traits that were used in the pioneering phase of the development of the breed (Scholtz and Ramsay, 2007). To gain some understanding of which traits were used and the emphasis put on them, two approaches could be used; 1) techniques based on finding out the owners/farmer's preferences (Tano *et al.,* 2003; Ndumu *et al*., 2008), or 2) an index describing the relative emphasis on each trait over the production period can be calculated in retrospect (Dickerson *et al*., 1954), where data are available.

The lack of participation in the national performance recording scheme until relatively recently leads to very little objective information and/or knowledge generated about the breed. It seems that within the breed society there are three schools of thought. The first group of breeders have a preventative approach and maintain that nature has been able to mould Nguni into an animal in complete harmony with its natural environment and further that it is difficult to improve a breed that has survived over centuries without the interference of man and adapted to the environment that it lives in (South African Livestock Breeding, 2004). This school of thought is consistent with Nguni being bred in the subsistence phase of production. The second group of breeders argues that Nguni lends sustainability to their enterprises. They believe that it is a resource that should help in food production while it should be maintained in a manner that it will still be able to provide food at the same level that it provides now or even better in the future. This is in agreement with both the *in situ* and *ex situ* conservation policies of the FAO (1998). According to the FAO (1998), *in-situ* conservation refers to the keeping of animals in the habitat and production systems that produced them whereas *ex-situ* refers to keeping animal outside the habitat and production systems that produced them. Operations following *in-situ* conservation also include performance recording schemes and development of breeding programs. *In-situ* conservation further includes ecosystem management and use of the sustainable production of food and agriculture (FAO, 1998). The third group holds the adaptation approach which maintains that nature will heal every change imposed on the breed and that the breed survived in the past and will continue to survive whether crossed or not. However, it is accepted that change due to any artificial selection including purifying, stabilizing, or performance-based criteria and natural selection in the new environment may alter gene frequencies in the gene pool (FAO, 1998).The main impediment to the resolution of these controversies has been a poor understanding of demographic and genetic factors (Lande, 1988). There has not been any study on the breed structure and genetic analysis of the breed. The study of the population structure and demography can highlight important circumstances affecting the genetic history of the population and indicate the relevant and appropriate managerial strategies into the future (Gama and Carolino, 2002).

With a breed society in place, but without formal pedigree information, it was a further challenge to establish a herd book and implement accepted breeding and selection procedures. The breed society had to implement relevant methodologies for the breeding of the Stud Nguni. These breeding strategies had to cope with the continuous immigration of animals from an uncontrolled environment to cater for the needs of the market, natural and stabilizing or purifying selection.

In search of appropriate approaches, existing strategies were tested. The usual technique for increasing numbers of “stud” animals within a breed, namely upgrading (Dalton, 1980), which had been used by other developing breeds like Bonsmara was thought not to be applicable as it was argued that the breed existed already (Scholtz and Ramsay, 2007). Top crossing coupled with phenotypic selection was the method of choice to introduce new genetic material from traditional breeders. However, the traditional farmers did not keep any records and pedigrees were important for registration purposes and performance evaluation. Thus, depth of pedigree (five generations) became the criterion by which phenotypically acceptable Nguni animals came to be recognized as “stud” Nguni.

In 1996, the Nguni was recognized as a developed breed, and the system changed to an appendix and SP (Studbook Proper) system. All animals of unknown parentage and those having known parents only that met the breed standards were recorded in Appendix A, those animals having known grandparents were recorded in Appendix B and those with deeper pedigrees were recorded as SP (Scholtz and Ramsay, 2007). Thus an animal sourced from the communal area would be recorded in Appendix A. The system promoted further immigration, in that a village animal, based solely on visual appraisal without pedigree came in as an "A" which is just two generations from being recorded as SP.

Despite the fact that exotic breeds brought into the villages by the previous government failed to adapt (Bester *et al*., 2003), after democratization in the country village people brought breeds and breed types of their choice into the village herd. Breeds such as Brahman, Bonsmara and Simmental were very popular. The village Nguni was kept in the same grazing land as the other breeds. Though there are arguments around the purity of the Nguni in villages, the breed society decided to put in strict measures governing immigrants coming into the breed in 2006 (Scholtz and Ramsay, 2007). The shift was from the emphasis on natural selection to stabilising or purifying selection. It led to the introduction of the concept of "First Registration" (FR) which is expected to serve as a filter. Within the system a multiple sire practice is permitted, however the products of the practice, irrespective of the generation stays an "A". An animal resulting from a multi-sire situation needs DNA verification to be classified as "B" or "SP". Restriction is placed on the sale of FR animals for stud breeding, to ensure that not only do they look like pure Nguni, but also, that they breed and perform like pure Nguni and meet the minimum breed standards. An FR cannot be transferred to another stud breeder as a registered animal.

### *2.2 Breeding objectives and selection index*

Breeding objectives developed from profit equations and empirical simulations may fail to account for some complexities in production systems (MacNeil and Matjuda, 2007). Such criticisms may be due to abstraction that is necessary to model the biological system and the dynamic nature of economic systems. James (1982) argued in favour of the breeding objectives and suggested that they should not be specified in too detailed a fashion. Also, Bright (1991), supporting James' (1982) views suggested that a simple profit equation may be sufficiently accurate in the short-term. Generally, for the breeding objectives to be useful they should be updated periodically in order to account for non-linearity that was not modeled and changes in the assumed economic structure (MacNeil and Matjuda, 2007). However, Pearson (1982) presented a countervailing argument that economic values be changed infrequently, after substantial evidence for changing price relationships has accumulated. Despite all contradictions in breeding objectives literature, MacNeil and Matjuda (2007) observed high genetic correlations among breeding objectives across sire and dam breeds.

A great deal of research had been reported on development of breeding programmes to increase biological and economic efficiency of livestock production (Dickerson, 1970; Harris, 1970; James 1982). When selection is applied for improvement of the economic value of the animal, it is simultaneously applied to several traits (Hazel, 1943; Newman *et al.*, 1992; Falconer and MacKay, 1996). Although the approaches vary, researchers agree that the development of breeding objectives is a crucial step in the development of breeding programmes (James, 1982; Ponzoni and Newman, 1989).

Literature include definitions of breeding objectives, the importance and usefulness of various approaches to estimation of economic values, areas of consensus, areas that are being debated, and the total evolution of the breeding objectives theory (Dickerson, 1970; Harris, 1970; James 1982; Van der Westhuizen and Matjuda, 1999). Kluyts *et al*. (2003), with some references to South Africa, provided a comprehensive review of procedures used in the development of breeding objectives. In this section, breeding objectives, selection index, types of economic values, approaches for estimating relative economic vales, usefulness of economic-based multiple-traits selection and relative economic values will be reviewed.

The breeding objective is a list of traits having economic value that the farmer would like to improve genetically. This list is based on the development objective of agricultural production and the characterisation of the animal production system. Each trait is given a goal value or relative economic weight indicating the contribution of the trait to the realisation of the development objective (Groen, 2000). Decisions about which traits should be included in the objective should be based on purely economic grounds, and not on whether they are difficult or easy to measure or to change genetically.

The definition of the breeding objective refers to the identification of important traits in the objective and their relative worth (Ponzoni and Newman, 1989). The breeding objective, towards which breeders are progressing, is therefore a particular combination of breeding values and the economic weighting factors for all the characters in the objective (Hazel, 1943; Falconer and MacKay, 1996; Bourdon, 1997). However, the breeding goal is not the final criterion or tool used in selection.

The tool used in deciding on which males and females will become parents of the next generation is the selection index. The selection index is a tool that lists all the observations for making the selection decisions. In the selection index observations are weighed by their coefficients. These index coefficients are calculated to maximise the correlation between the breeding objective and the selection index (Hazel, 1943; Groen, 2000). When the objective is maximum economic merit, the resulting index can appropriately be called an economic selection index (Gibson and Kenney, 1990).

Classically, selection toward a breeding objective is based on aggregate breeding value (H), which is a function of the summation of breeding values (a) for each for the n traits weighted by their respective economic values for trait (v). The relationship is

summarised as shown below (Hazel, 1943):

$$H = \sum_{i=1}^{n} v_i a_i$$

In practice, true breeding values may or may not be measurable, thus, H is estimated using a selection index (I), which is maximally correlated with H. The selection index is expressed through the following relationship (Hazel, 1943):

$$I = \sum_{j=1}^{m} b_j x_j$$

In this relationship, $b_j$ = a selection index weighting factor, $x_j$ = a phenotypic measure, and m = number of traits in the index. The optimum set of selection index coefficients are those which maximise the correlation ($r_{IH}$) or minimise the squared deviation between the selection index and the aggregate genotype.

In matrix notation the breeding objective would be H = v'a, where v is a n x 1 vector of economic values and a is a n x 1 vector of breeding values, given the n traits in the breeding objective. The index would be I = b´x, where x is a m x 1 vector of sources of information, b is a m x 1 vector of weighing factors. The elements of b are chosen to maximise genetic gain in aggregate breeding value or breeding objective. Hazel (1943) demonstrated that maximum $r_{IH}$ is achieved when Pb = Gv. Selection index weights are then calculated as b = $P^{-1}$Gv, where G is a n x m genetic covariance matrix for n traits affecting profitability and m correlated indicator traits and incorporates the additive genetic relationships between sources of information; P is a m x m phenotypic (co)variance matrix of correlated indicator traits; and v is a n x 1 vector of relative economic values.

Henderson (1963) demonstrated that the classical selection index (I) could also be expressed as follows:

$$I = \sum_{j=1}^{m} v_j \mathrm{EBV}_j$$

In the relationship, $v_j$ is the economic value from the breeding objective and $\mathrm{EBV}_j$ is the corresponding best linear unbiased prediction (BLUP) of the breeding value. The relationship simplifies continuous updating of trait information on all relatives, allows for direct comparison of animals with unequal amounts of information, and facilitates customized economic weights for individual breeds or breeders (Hazel *et al*., 1994).

When breeding values are not available for some economically important traits, extension of this index to include genetic evaluations for indicator traits is straightforward. Given appropriate estimates of genetic variances and covariances, this transformation to derive the weighting factors for the estimated BV is the product of partial regression coefficients for traits in the breeding objective on traits in the index and the economic values (Schneeberger *et al*., 1992). This development effectively divides prediction of H into two steps: (1) a bio-economic evaluation of the production system, and (2) a multiple-trait genetic evaluation. Currently, the latter technology is relatively well-developed in comparison to the former.

### *2.3 Definition and derivation of economic values*

Hazel (1943) in his classic paper defined an economic value as the change in the overall objective of one unit change in the trait while all other traits in the objective are kept constant. The derivation of economic values has been, in general, carried out with the assumption that the economic values are linear functions of trait values. Economic values so derived have been demonstrated to provide optimal selection criterion for linear profit functions (Goddard, 1998). Bright (1991) concluded that although economic values from simple linear profit function are sufficiently accurate, use of more empirically accepted non-linear equation should be considered. According to Pasternak and Weller (1993) no uniformly “best” index exists when economic values for some traits are not linear functions of trait values. They extended the method of Moav and Hill (1996) to derive optimum linear selection index which could be applied for linear or non-linear profit functions. In the context of dairy cattle, Dekkers and Gibson (1998) recommended the use of economic values derived from linear profit functions unless profit functions are extremely non-linear. While it is acknowledged that derivation of economic values depend on whether the profit function is linear or non-linear, the discussion of derivation of economic value in the ensuing sections focuses on derivation of economic values for linear profit functions. Economic values in the current study will therefore be derived for linear profit function.

The availability of resources for production and level of production vary among production units and enterprises. Therefore the relative economic values will differ from production unit to another. Harris and Newman (1994) proposed four alternative general traits having economic value to use in development of a breeding objective:

- cost of feed per unit weight
- cost of labour and facilities per unit time
- value per unit weight for product
- cost of initial animals

Cost of feed may be expanded to reflect differences in cost related to nutritive content. Value of product may be expanded to reflect differences in quality, such as body composition.

According to Newman *et al.* (1994), there are four basic approaches for estimating economic values, which are briefly reviewed below.

### *2.3.1 Budget based accounting*

The budget-based approach is based on the direct apportionment of cash flow to inputs and outputs. According to Pearson (1982: cited by Newman *et al*., 1992), the method is appealing for its simplicity and its independence from distributional properties of traits of economic importance. The early estimates of relative economic weights were derived by this method. In recent years, profit equations whose partial derivatives with respect to sources of income and expense can be taken as relative economic values have become the method of choice in some beef cattle breeding objective work, especially when a profit equation can be explicitly described (Ponzoni and Newman, 1989; Newman *et al*., 1992). Budget-based approaches may be of limited utility when functional relationships between traits for which data exist and those influencing inputs and outputs are complex or obscure.

### *2.3.2 Multiple regression techniques*

Multiple regression of profit on economically important traits provides an alternative means of obtaining relative economic values when budgeting income and expense are obscure (Hazel, 1943). The dependent variable is net profit, while the independent variables are the phenotypic traits. Thus, a partial regression coefficient of a trait indicates the change of net profit per unit change in each of the phenotypic traits when all other traits are held constant. The method is directly related to taking partial derivatives of the profit function with respect to each trait, and evaluating the derivatives at the mean of all other traits.

Unlike direct apportionment of cash flow, distributional properties of the economic values and of profit are of paramount importance. Partial regression coefficients are attractive when sources of cause and effect are recognized, but mechanisms inter-relating them are not established. Also, estimates of standard error of the economic values may be obtained. In this application, assumptions concerning completeness of the model, linearity of relationships and sampling from the intended population of inference may potentially be problematic, since estimates of the weights will be affected by the traits included in the description of net profit.

### *2.3.3 Ex-ante economic analysis*

Biologically-based models of production systems simulate relationships between inputs and outputs and facilitate ex-ante calculation of economic values, when prices of inputs and outputs are known. The approach may be viewed as a hybridization of the statistical prediction of profit and the budgeting approaches previously discussed. The main techniques used include scoring models, cost benefit methods, mathematical programming, and systems simulation. Use of simulation models, whether empirical or mechanistic, allows a more complete description of biological phenomena including potential tradeoffs between various traits. The complexity of a simulation model may require that relative economic values be approximated in some way. MacNeil and Newman (1992) calculated the sensitivity of profit to unit changes in driving variables as measures of respective relative economic values. Other researchers have conducted similar analyses with respect to state variables and / or have perturbed a controlling driving variable to obtain a unit change in the state variable of interest (Tess *et al.*, 1983a,b,c).

### *2.3.4 Econometric models*

Amer and Fox (1992) viewed genetic improvement as technological change in econometric framework. For instance, relative economic values can be estimated from parameters of a Cobb-Douglas production function for a meat production enterprise in accordance with this equation:

$$y = \alpha w B^{\beta} C^{\gamma}$$

In the above relationship, $w$ is the carcass weight of individual animals sold, $\alpha$ is a constant and exponents $\beta$ and $\gamma$ are partial elasticities of production from inputs $B$ and $C$, respectively. This proposed approach may require fewer restrictive assumptions than those discussed previously. However, this methodology shares the empiricism of multiple regressions. Extension of this methodology to incorporate mechanistic complexity of the production system may be anticipated.

### *2.4 Breeding objectives*

Every livestock producer has a goal. Though the goals may differ between producers, their overall goal is to increase their breeding objective (i.e., production, profitability, or sustainability). Ideally, the breeders in turn have to match their selection criteria to these objectives for their customers. The development of breeding objective is therefore a procedure that gives direction to a breeding program within a predefined production system that set out to contribute to the development objective of agricultural production (Sivarajasasingam *et al*., 1995).

Given the general agreement on the potential usefulness of breeding objective, the question must be raised as to why most breeders do not use economic breeding objectives (Newman *et al.*, 1994; Apiolaza and Garrick, 2001). Apiolaza and Garrick (2001) explored several issues that hinder the usefulness of breeding objectives in the tree industry and suggested that some of the problems affect the construction of the objective function, such as poor knowledge of the relationship between biological traits and end-product properties, uncertainty on both cost structure and future market prices. Other problems affect the application of the objective in selection process. A clear example would be the lack of good estimates of relationship between selection criteria and objective traits, and, finally, some problems impact on transforming gain in the objective into economic advantage for the industry like poor market signals between layers of the industry.

The best animal should be the animal that is best for the end user (Bourdon, 1998; Groen, 2000). Bourdon (1998) further argued that sometimes, the concept seems to get lost in the effort to satisfy expectations that really have little to do with the end user. Furthermore, Bourdon (1998) stated that this usually occurs at the level of the elite breeder. Bourdon (1998) attributes this distortion to competition among breeders. In an effort to convince buyers that her/his animals are superior to those of her/his competitors, she/he would emphasise traits that set her/his animals apart from the others, but may not be particularly important to her/his clients. The situation induces an undue reliance on the part of end users upon the opinions of breeders higher up in the pyramid.

The discussion on the distortion may create the impression that multiple–trait selection technology is available to the breeder as a product that can be obtained and used. Bourdon (1998) highlighted the paucity of such a product that can be obtained and used and that the only hindrance is at breeder level. Bourdon (1998) further highlighted the paucity of such a product by stating that genetic evaluation, as the term is used today in the beef cattle and sheep industries, refers to the calculation and dissemination of estimated breeding values (EBV) for individual traits. When the genetic evaluations are to be used wisely, genetic evaluation should be broadened to include multiple-trait selection technology, preferably technology that is customised for individual commercial and seedstock producers. Bourdon (1998) also stated that the problem is not that EBV are calculated incorrectly or with insufficient accuracy. The problem is that these predictions are presented without context. Newman *et al.* (1994) wrote that for healthier industries to occur, researchers must accept responsibility for developing the information through which their customer can access the added value of improved breeding stock. Genetic evaluation has taken the beef cattle industry a long way towards such an arrangement. The remaining task is to combine those EBV into a single-valued measure of an animal's worth to the customer for the customer's profit objective.

Economic-based multiple-trait selection procedures have potential usefulness in the beef industry because (1) the breeder can use that combination of EBV that will maximise genetic progress for least recording effort and processing cost, (2) breeding can be used to target several markets, (3) breeders can use genetic evaluation more efficiently, since breeding involves more than one trait; indices will facilitate selection for traits associated with the economics of production, (4) breeders can address the needs of the commercial sector, which should allow for separate rankings for different types of commercial producers, and (5) indices can promote increase in genetic gain in profit for users and industry via dissemination of genes better targeted for profit in commercial herds (Newman *et al.,* 1994).

Deciding upon the breeding goal, the user first needs to establish in what direction the agricultural production in the country is to change. Before doing so, two important dimensions of decision making in agricultural production should be considered, namely level and time horizon. From a national perspective, the traits in the breeding objective may be viewed as outputs or products to be used in achieving an outcome based on the country's development objective for agricultural production. The same traits may be viewed as an end product or output that generate income to maximise profit for the farmer (Groen, 2000).

The statement in the above paragraph brings forth a new concept namely interest of selection (Groen, 2000). Interest of selection denotes the primary interest of the decision-maker, with three options:

- Profit maximisation, which is mainly the farmer's interest,
- Most price minimisation, which is mostly the government's interest, and
- Maximise return on investment, which is mainly an investor's interest.

The primary interest will strongly depend upon the position that the decision-maker holds in the community, market or industry. Generally, any decision-maker has to contend with legislative, environmental, economic, political and social factors, which shape the ultimate selection of the option taken. The cited factors are the primary elements of sustainable production (Olesen *et al*., 2000).

Genetic merit is tied to the animal level but interests above the animal level may be considered as well (Groen, 2000). Therefore, the animal level is the lowest level considered in deriving relative economic values, Olesen *et al.* (2000) suggested that a model of different perspectives, world views, informed by a specific ontology, that is the way we see nature and epistemology, which is the way humans try to learn about nature, should be considered in relative economic values.

The discussion above may suggest that the theoretically appropriate level to be used in deriving relative economic values is the one for which limited resources and prices of product and resources are influenced by an improvement of the trait. By implication these levels are both sector and / or national level. The perspectives belong to levels above the animal level.

Elements and their relationships chosen in a model on animal level depend on biological processes at even lower levels (Groen, 2000). However theoretically appropriate levels, national and sector levels are rarely chosen because of methodological difficulties. When breeding objectives have been developed by and for producers or groups of producers, emphasis is therefore put on profit maximisation, with the consequence that the farmer is therefore advised/compelled to opt for profit. Furthermore, Groen (2000) argued that the potential bias as a result of the simplification made by modelling at herd or farm level can be tested by calculating relative economic values for several assumptions on market prices and production levels.

## *2.5 Index in retrospect*

Van Vleck (1993) provided a detailed explanation of index-in-retrospect, which will only be summarised in this review. The index-in-retrospect is the method that could be used to determine whether there were any gains made in the past for traits of economic importance. The index-in-retrospect is an index that might have been used for selection to produce gains that have occurred even though the weights for the index might have been unknown at the time of selection (Van Vleck, 1993: citing Dickerson *et al.*, 1954). Determining the index that might have been used depends on finding an index which would have given the set of phenotypic selection differentials actually observed. The index is calculated as follows:

$$I = \sum_{j=1}^{m} w_j P_j$$

In the above relationship, the index corresponds to that which would have been used for selection given the observed changes in traits. Further, define D as the selection intensity factor. The phenotypic record for trait j measured on the animal being selected is $P_j$. When the underlying unknown index is I, the regression of $P_j$ on I gives the expected phenotypic selection response for trait (Van Vleck, 1993). Since $D/\sigma_I$ is a constant for all traits, the proportionality of the right-hand sides for different traits will not change. Both D and I, however, may be different for males and females and even from generation to generation. Indices in retrospect can be computed separately for males and females and for each generation. The expectations of the N phenotypic selection differentials are as follows (Van Vleck, 1993):

$$E[\Delta P_1] = Cov(P_1, I) = w_1\sigma^2_{P_1} + w_2\sigma_{P_1P_2} + \ldots + w_N\sigma_{P_1P_N}$$

$$E[\Delta P_2] = Cov(P_2, I) = w_1\sigma_{P_1P_2} + w_2\sigma^2_{P_2} + \ldots + w_N\sigma_{P_2P_N}$$

$$.$$

$$.$$

$$.$$

$$E[\Delta P_N] = Cov(P_N, I) = w_1\sigma_{P_1P_N} + w_2\sigma_{P_2P_N} + \ldots + w_N\sigma^2_{P_N}$$

The coefficients of the w's are the same as for finding the best selection index weights, i.e, the phenotypic variances and covariances. The selection differentials ($\Delta P_j$) can be equated to their expectations. In other words, the left hand sides of the usual selection index equations would determine in retrospect the relative weights for the index. The symbol w is used for the weights for the index-in-retrospect. The phenotypic variances and covariances must be known as well as the phenotypic selection differentials (Van Vleck, 1993). A linear index in the phenotypic values is assumed as in truncation selection based on the underlying but unknown index.

In matrix notation $w = P^{-1}\Delta p$ where w is the vector of retrospective weights, P is the phenotypic variance-covariance matrix, and $\Delta p$ is the vector of phenotypic selection differentials (Van Vleck, 1993). The relative expected genetic responses from using the retrospective index are: $\Delta G_j = (D/\sigma_I) \text{ Cov } (G_j, I)$ for $j = 1, \ldots, N$ which could be compared with the expected responses for the theoretically best index for which economic values are assumed known.

## 2.6 Summary

This chapter indicates that the theory for the development of breeding objectives in beef cattle is relatively well developed. There is also general agreement among animal breeders about the importance of breeding objectives. However, breeding objectives for most beef cattle populations are not defined in general and for the Nguni cattle breed in particular. Therefore, the development of breeding objectives for the Nguni cattle remains an important step towards delivery of a multiple-trait selection technology for the breeders.

# CHAPTER 3

# BREED STRUCTURE AND GENETIC ANALYSIS OF THE PEDIGREED NGUNI CATTLE IN SOUTH AFRICA

### *3.1 Introduction*

Nguni, a Sanga breed, is well-adapted to the Southern African environment (Meyer, 1984.) Originally the name Nguni referred to Swazi, Zulu and Landim cattle of Mozambique (Rege and Tawah, 1999). The origin of the breed is speculative, but it has been acknowledged that the breed has been in the ownership of traditional black farmers for centuries (Scholtz and Ramsay, 2007). The breed is spread throughout the Southern African region and is made up of several ecotypes (South African Livestock Breeding, 2004). While Nguni has historically been restricted to village or communal husbandry, it has recently become recognized as an established breed with the associated breed society implementing pedigree and performance recording. Based on the recorded pedigree and performance data the Agricultural Research Council estimated that current participation in the national beef cattle performance recording programs accounts for approximately 27% of Nguni breeders (National Beef Recording and Improvement Scheme, 2007).

The purpose of the study is to determine the demographic and genetic structures of the Nguni population. These analyses focus on quantifying characteristics unique to the population as opposed to individuals. Population analysis is usually done for purposes of recording breed history and/or planning future breeding schemes. It can be divided into two main major categories viz. 1) demographic analysis, involving such things as birth and death rates, growth rates (numbers and/or biomass), age structure, sex ratio, average longevity and life history production, 2) Genetic analysis focus on patterns of genetic contributions from generation to generations. Genetic breed analyses have been performed by describing the population through calculation of generation intervals, inbreeding coefficients, and effective population size (Schons *et al.,* 1985). Results may be used to parameterize various simulation models for study of both management and genetic approaches to practical questions and enhance the well-being of farmers raising Nguni cattle.

### *3.2 Materials and methods*

Pedigree data of recorded and registered Nguni animals born between 1973 and 2006 were obtained from the Agricultural Research Council (ARC) for this study. The data included 142,622 records of animal, sire, and dam identification numbers, gender and birth year. The data were collected in two periods, prior to and after formation of the breed society. Data from the period 1973 to 1985 which was prior to formation of the breed society was collected on well managed farms (mostly government experimental stations) and assembled in the herdbook in 1986 (Scholtz and Ramsay, 2007). Pedigrees were checked for integrity and records of 8 bulls first appearing as sires of 22 progeny were removed. Table 3.1 summarizes the structure of the data after editing.

Two sets of analyses were carried out in the current study. The set of first analyses evaluated the demographic structure of the recorded Nguni population. The second set of analyses calculated statistics related to the effective population size of the Nguni breed.

**Table 3.1** Numbers of sires and dams present in the Nguni pedigree and classifications of animals with various amounts of known pedigree information.

| Item | Number of Sires | Number of Dams | At least 1 parent known | Both parents known | Sire known | Dam known | Unknown Parents |
|---|---|---|---|---|---|---|---|
| Number of records | 2623 | 23327 | 112108 | 98743 | 100609 | 110242 | 30514 |

### *3.2.1 Demographic statistics*

Data of all animals from the Nguni herdbook was used to compile: 1) the numbers of offspring recorded each year and their parents; 2) the number and proportion of the recorded sires and dams that produced progeny that subsequently became parents; 3) age distribution of South African Nguni males in reproduction by year of birth of their offspring, 4) age distribution of South African Nguni females in reproduction by year of birth of their offspring, 5) distribution of females by parity number. The Nguni herdbook is not closed and therefore animals with Nguni blood could be brought into the breed using the appendix system of registration. Embryo transfer technology is used in the Nguni breed which will influence the dam family sizes.

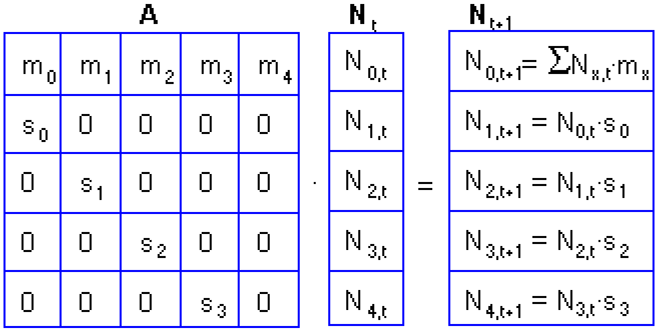
For population growth projections the model of Leslie (1945, 1948) was used. The model describes three kinds of ecological processes 1) development (progress through the life cycle), 2) age-specific mortality 3), and age-specific reproduction.

- $N_{x,t}$ = number of organisms of age *x*, at time *t* (age is measured in the same units as time *t*). Usually, only females are considered and males are ignored because, as a rule, the number of males does not affect population growth;
- $S_x$ = survival of organisms in age interval from *x* to *x*+1; and
- $M_x$ = average number of female offspring produced by 1 female in age interval from *x* to *x*+1 (mortality of parent and/or offspring organisms is included).

Then:

$$A \bullet N_t = N_{t+1}$$

As an example, for *t* = 4:



$$\begin{array}{ccccc}
\mathbf{A} & & \mathbf{N}_t & & \mathbf{N}_{t+1} \\
\begin{array}{|c|c|c|c|c|}\hline m_0 & m_1 & m_2 & m_3 & m_4 \\ \hline s_0 & 0 & 0 & 0 & 0 \\ \hline 0 & s_1 & 0 & 0 & 0 \\ \hline 0 & 0 & s_2 & 0 & 0 \\ \hline 0 & 0 & 0 & s_3 & 0 \\ \hline \end{array} & \cdot &
\begin{array}{|c|}\hline N_{0,t} \\ \hline N_{1,t} \\ \hline N_{2,t} \\ \hline N_{3,t} \\ \hline N_{4,t} \\ \hline \end{array} & = &
\begin{array}{|c|}\hline N_{0,t+1} = \sum N_{x,t} \cdot m_x \\ \hline N_{1,t+1} = N_{0,t} \cdot s_0 \\ \hline N_{2,t+1} = N_{1,t} \cdot s_1 \\ \hline N_{3,t+1} = N_{2,t} \cdot s_2 \\ \hline N_{4,t+1} = N_{3,t} \cdot s_3 \\ \hline \end{array}
\end{array}$$

Census data were used to develop model parameters for females first exposed for breeding either as yearlings or 2-year-olds. Maximum age for females in reproduction was set to 15 years. Total number of breeding females was fixed at 1000 by altering survival of the first age class (S0) to reflect additional females being sold.

### *3.2.2 Genetic statistics*

In order to summarize the genetic make-up of the recorded Nguni population the following statistics were calculated: 1) generation number relative to the first recorded ancestor and generation interval for each of the four different selection paths, 2) minimum, maximum, mean, and variance of family size, and 3) inbreeding coefficient relative to first recorded ancestor**.**

Computation of the generation number was carried out as follows:

1. Unknown parents were assumed to belong to generation 0;
2. For each recorded animal, its generation number was the average generation number of its parents + 1;

Transfer of genes from parents to offspring occurs through four pathways: sires to sons (SS), sires to daughters (SD), dams to sons (DS) and dams to daughters (DD). Thus, the generation intervals (L) for each pathway were computed as the difference between the generation number of an offspring that ultimately became a parent and the generation number of its parent. The population generation intervals were computed using the formula:

$$L = (L_{ss} + L_{sd} + L_{ds} + L_{dd})/4$$

Inbreeding coefficients were calculated using the method put forth by Quaas (1976). For this calculation the base population was assumed to be those animals that were the unknown parents of generation 1.

Effective population size ($N_e$) was calculated from the change in inbreeding per generation obtained from multiplying the annual rate of inbreeding, $\Delta F_{y,}$ with the generation interval (L), as follows (Cleveland *et al.*, 2005):

$$N_e = 1/(2 \bullet \Delta F_y \bullet L)$$

To examine the current status of the South African Nguni population animals born from 2004 to 2006 were considered. This group is characterized by having all ancestors known for at least 3 generations. The annual change in mean inbreeding ($\Delta F_y$) was calculated as the regression of inbreeding coefficient on birth year (Cleveland *et al*., 2005).

## *3.3 Results*

### *3.3.1 Demographic statistics*

Numbers of animals with different amounts of known pedigree are summarized in Table 3.1. The high number of animals with unknown parents results from immigration of Nguni-type animals from the villages and communal areas. The difference between the calves with unknown sires and unknown dams may be due to the multi-sire system. The unknown dams are immigrants who are not registered and are joined with registered bulls and thus give birth to registered calves whose sires are known. Both the multi-sire system and immigrants contribute to the class of calves with at least 1 known parent.

Presented in Table 3.2 are the total numbers of calves recorded and degree to which their pedigree was known, numbers of their recorded parents, and numbers of those parents whose offspring subsequently became parents themselves, arrayed by birth year of their offspring in the Nguni population from 1973 to 2006. For example, in 1986, 2440 calves were recorded, with 132 known sires and 1463 known dams. However, only the offspring of 100 sires and 383 females became parents of recorded progeny. The sire of 1525 of the calves was known, while 1504 of the dams were known. For birth years 2004 to 2006, the progeny of the sires and dams had not yet had an opportunity to become parents themselves and these data are hence missing.

The number of calves with sire and dam unknown increased annually with the increasing number of calves born from 1986 to 2004. The annual percentage of calves with unknown sire fluctuated from 20 to 39%, for the period 1986 to 2004. For the same period, the percentage of calves with unknown dam has fluctuated from 16 to 40%. The high numbers of calves with one parent known is probably due to immigration and breeding in multiple sire situations. This is due in part to the practice of always declaring the sire unknown when the calf results from a multi-sire situation.

With immigrants, cows were often joined with a registered sire and the calves would then be registered with dam unknown. According to breed society policy implemented in the 2005/2006 immigrants were brought in at the first registration (FR) level, whereas previously they were recorded in Appendix A. This prompted the breeders to register all their Nguni-type commercial cows as “A” before the implementation of the change. As a result, there was a marked reduction in the number of calves with unknown sire from 3230 in 2004 to 1960 in 2005 which was a reduction from 31 to 20%. For calves with dam unknown the reduction was from 2157 in 2004 to 544 in 2005. In 2006, calves with unknown dams were only 0.18% of all recorded calves**.**

Since establishment of the herdbook in 1986 to 2002, the proportion of sires whose offspring subsequently became parents fluctuated between 53 and 76%, with an average of 60% (Table 3.3). For dams, the percentage whose offspring becomes parents fluctuates between 13 and 26% with an average of 19%. Data from 2003 and 2004 were not included in the calculation of these averages because the low numbers reported in Table 3.2 indicate that not all the birth notifications for the years in which descendants born in these years would be parents had been captured. These percentages demonstrate that genetic progress in the subsequent generations was influenced by about 60% of the bulls; whereas the influence from the female side was about 20%.

**Table 3.1** Number of sires and dams and recorded in the South African Nguni herdbook, by year of birth of offspring.

| | Sires | | Dams | | Number of Animals | | |
|---|---|---|---|---|---|---|---|
| **Year** | With progeny[1] | Producing parents[2] | With progeny | Producing parents | Born | With known sire | With Known dam |
| **1973** | 1 | 1 | . | . | 48 | 2 | 0 |
| **1974** | 1 | 1 | . | . | 92 | 2 | 0 |
| **1975** | 1 | 1 | . | . | 111 | 2 | 0 |
| **1976** | 1 | 1 | . | . | 112 | 2 | 0 |
| **1977** | 1 | 1 | 3 | 3 | 159 | 3 | 3 |
| **1978** | 1 | 1 | 7 | 5 | 218 | 5 | 7 |
| **1979** | 4 | 4 | 5 | 5 | 445 | 16 | 5 |
| **1980** | 4 | 4 | 16 | 15 | 425 | 14 | 16 |
| **1981** | 10 | 9 | 23 | 22 | 429 | 41 | 23 |
| **1982** | 18 | 16 | 47 | 43 | 594 | 88 | 47 |
| **1983** | 26 | 24 | 85 | 66 | 794 | 114 | 85 |
| **1984** | 61 | 53 | 251 | 172 | 1044 | 284 | 251 |
| **1985** | 92 | 74 | 1173 | 326 | 2272 | 1242 | 1182 |
| **1986** | 132 | 100 | 1463 | 383 | 2440 | 1525 | 1504 |
| **1987** | 170 | 119 | 1682 | 404 | 2866 | 1741 | 1706 |
| **1988** | 214 | 141 | 2458 | 510 | 3697 | 2505 | 2500 |
| **1989** | 274 | 156 | 2939 | 543 | 4164 | 3011 | 2984 |
| **1990** | 282 | 163 | 3227 | 589 | 4628 | 3320 | 3307 |
| **1991** | 297 | 153 | 3483 | 543 | 4471 | 3539 | 3545 |
| **1992** | 322 | 170 | 3568 | 478 | 4869 | 3612 | 3623 |
| **1993** | 326 | 169 | 3123 | 651 | 4603 | 2937 | 3157 |
| **1994** | 337 | 196 | 3704 | 791 | 5476 | 3513 | 3809 |
| **1995** | 339 | 197 | 3966 | 742 | 5520 | 3543 | 4018 |
| **1996** | 331 | 218 | 4618 | 892 | 5958 | 4140 | 4725 |
| **1997** | 384 | 234 | 4828 | 924 | 6077 | 4527 | 4892 |
| **1998** | 432 | 272 | 5488 | 1046 | 6664 | 5321 | 5576 |
| **1999** | 445 | 266 | 5629 | 1065 | 7025 | 5312 | 5739 |
| **2000** | 427 | 258 | 5684 | 1175 | 7163 | 5114 | 5793 |
| **2001** | 443 | 284 | 6408 | 1221 | 8107 | 5621 | 6531 |
| **2002** | 469 | 272 | 6648 | 1142 | 8690 | 6187 | 6874 |
| **2003** | 497 | 178 | 7372 | 519 | 9786 | 6756 | 7559 |
| **2004** | 560 | 31 | 8055 | 36 | 10436 | 7206 | 8279 |
| **2005** | 550 | - | 9218 | - | 10036 | 8076 | 9492 |
| **2006** | 697 | - | 11611 | - | 11974 | 10418 | 11952 |

---

[1] With progeny = Number of parents producing progeny in the specified year.

[2] Producing parents = Number of parents whose progeny subsequently became parents themselves.

**Table 3.2** Percent of recorded sires and dams contributing progeny to the subsequent generation, beginning with the establishment of the Nguni herd-book in 1986.

| Year | Bulls, % | Cows, % |
|---|---|---|
| 1986 | 75.75 | 26.17 |
| 1987 | 70.00 | 24.01 |
| 1988 | 65.88 | 20.74 |
| 1989 | 56.93 | 18.47 |
| 1990 | 57.80 | 18.25 |
| 1991 | 51.51 | 15.83 |
| 1992 | 52.79 | 13.39 |
| 1993 | 51.84 | 20.84 |
| 1994 | 52.16 | 21.34 |
| 1995 | 58.11 | 18.70 |
| 1996 | 65.86 | 19.31 |
| 1997 | 60.93 | 19.13 |
| 1998 | 62.96 | 19.05 |
| 1999 | 59.77 | 18.91 |
| 2000 | 60.42 | 20.67 |
| 2001 | 64.10 | 19.05 |
| 2002 | 57.99 | 17.17 |
| 2003 | 36.81 | 7.04 |

Shown in Table 3.4 is the age distribution of Nguni sires arrayed by birth year of their offspring. Although they are included in the table, one and two year old sires were not considered further because Nguni bulls cannot be registered before the age of two years. These animals may have been immigrants whose ages were estimated. Since the establishment of the herd book in 1986, most calves have been sired by bulls 3 to 8

**Table 3.3** Age distribution of South African Nguni sires by year of birth of their offspring.

| | Age in Males in Years | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **μ** |
| **1974** | | | | | | | 1 | | | | | | | | | | | | | | | | | | 7.0 |
| **1975** | | | | | | | | 1 | | | | | | | | | | | | | | | | | 8.0 |
| **1976** | | | | | | | | | 1 | | | | | | | | | | | | | | | | 9.0 |
| **1977** | | | | | | | | | | 1 | | | | | | | | | | | | | | | 10.0 |
| **1978** | | | | | | | | | | | 1 | | | | | | | | | | | | | | 11.0 |
| **1979** | | | | 1 | 1 | 2 | | | | | | 1 | | | | | | | | | | | | | 6.6 |
| **1980** | | | 1 | 1 | | 1 | 1 | | | | | | | | | | | | | | | | | | 5.0 |
| **1981** | | 3 | 1 | 1 | 2 | | 1 | 2 | | | | | | | | | | | | | | | | | 4.6 |
| **1982** | | 2 | 2 | 3 | 1 | 2 | 2 | 4 | 1 | | | | | | 1 | | | | | | | | | | 6.1 |
| **1983** | | | 6 | 4 | 4 | 4 | 3 | 1 | 2 | 1 | | | | | | 1 | | | | | | | | | 5.8 |
| **1984** | | | 6 | 15 | 11 | 9 | 8 | 2 | 4 | 3 | 2 | | | | | | 1 | | | | | | | | 6.0 |
| **1985** | 1 | 4 | 14 | 21 | 15 | 11 | 11 | 4 | 4 | 3 | 2 | 2 | | | | | | | | | | | | | 5.4 |
| **1986** | 2 | 7 | 22 | 22 | 22 | 17 | 9 | 12 | 6 | 4 | 4 | 3 | 2 | | | | | | | | | | | | 5.6 |
| **1987** | | 9 | 24 | 31 | 27 | 23 | 19 | 11 | 11 | 3 | 4 | 2 | 3 | 2 | | | | | | 1 | | | | | 5.7 |
| **1988** | 2 | 7 | 39 | 54 | 32 | 22 | 20 | 15 | 6 | 5 | 3 | 3 | 2 | 2 | 2 | | | | | | | | | | 5.4 |
| **1989** | | 8 | 27 | 75 | 63 | 35 | 19 | 14 | 12 | 6 | 5 | 2 | 2 | 2 | | 2 | | | | | | | | | 5.5 |
| **1990** | | 12 | 43 | 47 | 66 | 49 | 23 | 13 | 9 | | 8 | 4 | 2 | 2 | 2 | | | | | | | | | | 5.5 |
| **1991** | | 6 | 43 | 59 | 51 | 54 | 39 | 16 | 12 | 5 | 4 | | 4 | 2 | | | | | | | | | | | 5.6 |
| **1992** | | 9 | 42 | 74 | 51 | 51 | 43 | 22 | 12 | 11 | 2 | 2 | | 3 | | | | | | | | | | | 5.5 |
| **1993** | | 6 | 42 | 57 | 70 | 44 | 41 | 29 | 20 | 7 | 4 | | 2 | | 3 | | | | | | | | | | 5.7 |
| **1994** | 1 | 8 | 28 | 62 | 57 | 71 | 32 | 29 | 24 | 13 | 6 | 4 | 1 | | | | | | | | | | | | 5.9 |
| **1995** | 1 | 4 | 45 | 52 | 59 | 43 | 65 | 24 | 18 | 12 | 5 | 5 | 4 | 1 | | | | | | | | | | | 6.0 |
| **1996** | | 12 | 49 | 60 | 50 | 50 | 33 | 39 | 15 | 9 | 6 | 4 | 2 | 1 | | | | | | | | 1 | | | 5.7 |
| **1997** | | 11 | 65 | 71 | 67 | 44 | 47 | 24 | 22 | 14 | 10 | 4 | 4 | | | | | | | | | | 1 | | 5.6 |
| **1998** | 1 | 17 | 60 | 92 | 69 | 48 | 47 | 38 | 17 | 22 | 6 | 8 | 2 | 4 | | | | | | | | | | 1 | 5.8 |
| **1999** | 2 | 15 | 67 | 84 | 81 | 61 | 43 | 26 | 26 | 12 | 15 | 4 | 6 | 1 | 1 | | | | | | | | | | 5.7 |
| **2000** | 2 | 13 | 56 | 105 | 65 | 51 | 48 | 28 | 17 | 14 | 7 | 14 | 2 | 2 | 1 | 1 | | | | | | | | | 5.7 |
| **2001** | 1 | 9 | 54 | 86 | 103 | 53 | 40 | 35 | 21 | 12 | 10 | 6 | 6 | 1 | 2 | 1 | 1 | | | | | 1 | | | 5.9 |
| **2002** | | 11 | 40 | 99 | 78 | 90 | 49 | 33 | 24 | 14 | 7 | 7 | 4 | 6 | 2 | 1 | 2 | 1 | | | | | | | 6.0 |
| **2003** | 2 | 12 | 63 | 69 | 100 | 71 | 59 | 40 | 28 | 22 | 10 | 9 | 5 | 3 | | 1 | | | | | | | | | 6.0 |
| **2004** | 1 | 5 | 61 | 109 | 78 | 90 | 62 | 51 | 35 | 23 | 19 | 9 | 8 | 6 | 1 | | | | | | | | | | 6.2 |
| **2005** | 1 | 12 | 59 | 99 | 98 | 67 | 67 | 51 | 31 | 24 | 12 | 12 | 6 | 5 | 2 | 1 | | | | | | | | | 6.1 |
| **2006** | | 21 | 68 | 148 | 111 | 98 | 62 | 61 | 45 | 23 | 22 | 11 | 10 | 4 | 3 | 2 | 3 | 1 | 1 | | | | | | 6.1 |

years of age. The average age of the sires during this period has been 5.8 years. However, the modal age of sire has been younger; most frequently 4 years.

Shown is Table 3.5 is the age distribution of Nguni dams arrayed by birth year of their offspring.  The one-year-old dams were not considered further as it is believed that these few individuals reflect mistakes in the data. There were sizeable numbers of females that calved at two years of age. However, the modal age of dam was three years, with a steady decline thereafter. Three-year old dams being most frequent is a result of dams that calved for the first time at the age of two years calving again at three and additional females calving for the first time at three years of age. This result arises from some farmers preferring a three years age of first calving while others prefer two years for age at first calving. The average age of dam was 5.5 years. The difference between the average age of females and males when their progeny are born is only 0.2 years.

Table 3.6 presents the distribution of parities attained by dams of Nguni calves recorded in the South African herdbook arrayed over years and the average number of parities achieved by dams producing recorded progeny each year. There were more calves from third parity dams than from dams with any other number of parities. Relatively few calves out of first parity dams were recorded. The number of calves recorded from dams with more than three parities decreases with time, as expected. Groeneveld (2007) argues that dams with parity $\geq$ 16 years are often few in the population and they conveniently placed together in one group. However, adding up numbers of dams with

**Table 3.4** Age distribution of South African Nguni dams by year of birth of their offspring.

| | Age of Dam, years | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** | **μ** |
| **1978** | | | 2 | 4 | 1 | | | | | | | | | | | | | | | | | | | | | | 3.9 |
| **1979** | | | | 2 | 3 | | | | | | | | | | | | | | | | | | | | | | 4.6 |
| **1980** | | 1 | 4 | | | 6 | 2 | | 1 | 1 | | 1 | | | | | | | | | | | | | | | 5.9 |
| **1981** | | 3 | 3 | 4 | 1 | 4 | 5 | | 2 | | | | 1 | | | | | | | | | | | | | | 5.5 |
| **1982** | | 2 | 13 | 7 | 6 | | 6 | 5 | 1 | 3 | | 2 | | 1 | | 1 | | | | | | | | | | | 5.9 |
| **1983** | 3 | 5 | 22 | 18 | 5 | 8 | 3 | 5 | 10 | 1 | 2 | 1 | | | | | 2 | | | | | | | | | | 5.3 |
| **1984** | 15 | 18 | 49 | 35 | 38 | 23 | 14 | 16 | 8 | 7 | 4 | 3 | 2 | 8 | 3 | 8 | | | | | | | | | | | 5.7 |
| **1985** | 16 | 98 | 194 | 133 | 140 | 186 | 102 | 73 | 44 | 54 | 35 | 26 | 19 | 11 | 25 | 7 | 7 | | 3 | | | | | | | | 6.1 |
| **1986** | 18 | 83 | 277 | 202 | 143 | 144 | 218 | 93 | 73 | 42 | 51 | 37 | 25 | 20 | 10 | 21 | 1 | 4 | | 1 | | | | | | | 6.1 |
| **1987** | 10 | 153 | 267 | 255 | 209 | 137 | 132 | 189 | 81 | 73 | 35 | 49 | 25 | 20 | 12 | 8 | 19 | 4 | 3 | | 1 | | | | | | 6.1 |
| **1988** | 41 | 220 | 561 | 332 | 247 | 208 | 155 | 150 | 182 | 94 | 72 | 47 | 50 | 30 | 25 | 12 | 5 | 20 | 2 | 4 | | 1 | | | | | 5.9 |
| **1989** | 18 | 256 | 535 | 550 | 384 | 248 | 215 | 174 | 140 | 151 | 90 | 61 | 32 | 32 | 20 | 9 | 2 | 2 | 15 | 3 | 1 | | 1 | | | | 5.7 |
| **1990** | 5 | 323 | 594 | 479 | 493 | 360 | 227 | 188 | 141 | 112 | 130 | 58 | 43 | 19 | 19 | 12 | 11 | 3 | 1 | 9 | | | | | | | 5.7 |
| **1991** | 6 | 229 | 718 | 548 | 440 | 407 | 307 | 204 | 172 | 123 | 89 | 98 | 50 | 37 | 15 | 18 | 7 | 4 | 2 | 1 | 7 | 1 | | | | | 5.8 |
| **1992** | 9 | 277 | 843 | 546 | 444 | 327 | 293 | 229 | 162 | 126 | 90 | 65 | 59 | 35 | 28 | 10 | 11 | 5 | 3 | 1 | | 5 | | | | | 5.6 |
| **1993** | 8 | 180 | 716 | 524 | 381 | 346 | 256 | 202 | 160 | 106 | 74 | 47 | 35 | 41 | 17 | 12 | 5 | 3 | 6 | | | 1 | 3 | | | | 5.7 |
| **1994** | 12 | 250 | 703 | 635 | 509 | 376 | 336 | 250 | 190 | 129 | 108 | 62 | 45 | 27 | 31 | 13 | 17 | 3 | 3 | 2 | | | | 3 | | | 5.8 |
| **1995** | 13 | 372 | 812 | 533 | 573 | 432 | 325 | 271 | 226 | 145 | 82 | 72 | 36 | 22 | 23 | 14 | 5 | 5 | | 3 | 2 | | | | | | 5.6 |
| **1996** | 29 | 529 | 986 | 751 | 496 | 486 | 408 | 285 | 237 | 141 | 94 | 67 | 40 | 25 | 14 | 13 | 6 | 5 | 3 | 2 | 1 | | | | | | 5.3 |
| **1997** | 25 | 522 | 1015 | 773 | 613 | 437 | 419 | 316 | 257 | 154 | 126 | 68 | 46 | 21 | 13 | 8 | 11 | 3 | | | | 1 | | | | | 5.4 |
| **1998** | 18 | 577 | 1090 | 932 | 680 | 560 | 401 | 385 | 307 | 182 | 121 | 104 | 62 | 38 | 12 | 6 | 4 | 4 | 2 | | | | 2 | | | 1 | 5.4 |
| **1999** | 16 | 561 | 1009 | 859 | 844 | 574 | 462 | 330 | 330 | 244 | 160 | 89 | 74 | 39 | 26 | 5 | 1 | 3 | 3 | | | | | | | | 5.6 |
| **2000** | 18 | 529 | 1039 | 811 | 731 | 722 | 458 | 376 | 265 | 249 | 181 | 128 | 63 | 59 | 30 | 17 | 4 | | 1 | 3 | | | | | | | 5.7 |
| **2001** | 16 | 638 | 1227 | 899 | 747 | 640 | 660 | 407 | 317 | 239 | 211 | 168 | 112 | 51 | 42 | 20 | 9 | 1 | 1 | | 3 | | | | | | 5.8 |
| **2002** | 24 | 640 | 1267 | 933 | 805 | 663 | 543 | 567 | 337 | 247 | 186 | 153 | 126 | 76 | 29 | 33 | 14 | 6 | 2 | | | 1 | | | | | 5.8 |
| **2003** | 17 | 740 | 1365 | 1150 | 932 | 735 | 602 | 480 | 504 | 253 | 198 | 138 | 100 | 79 | 41 | 17 | 17 | 2 | | 2 | | | | | | | 5.7 |
| **2004** | 58 | 840 | 1494 | 1213 | 1066 | 853 | 658 | 500 | 402 | 371 | 212 | 144 | 86 | 65 | 47 | 24 | 13 | 6 | 2 | | 1 | | | | | | 5.6 |
| **2005** | 105 | 1132 | 1752 | 1416 | 1141 | 953 | 720 | 561 | 425 | 364 | 257 | 146 | 89 | 63 | 47 | 26 | 17 | 2 | 1 | | | 1 | | | | | 5.4 |
| **2006** | 57 | 1421 | 2280 | 1728 | 1439 | 1161 | 945 | 735 | 573 | 394 | 342 | 232 | 112 | 82 | 45 | 27 | 18 | 13 | 4 | 1 | | | | | | 1 | 5.5 |

**Table 3.5** Distribution of parity number for dams of Nguni calves recorded in the South African herdbook.

| | Parity Number | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Year** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** | **23** | **24** | **25** | **26** |
| **1977** | | | 2 | | | 1 | | | | | | | | | | | | | | | | | | | | |
| **1978** | | | 2 | 4 | 1 | | | | | | | | | | | | | | | | | | | | | |
| **1979** | | | | 2 | 3 | | | | | | | | | | | | | | | | | | | | | |
| **1980** | | 1 | 4 | | | 6 | 2 | | 1 | 1 | | 1 | | | | | | | | | | | | | | |
| **1981** | | 4 | 4 | 4 | 1 | 5 | 5 | | 2 | | | | 1 | | | | | | | | | | | | | |
| **1982** | | 2 | 16 | 7 | 7 | | 7 | 5 | 1 | 3 | | 2 | | 1 | | 1 | | | | | | | | | | |
| **1983** | 3 | 5 | 24 | 21 | 5 | 10 | 3 | 5 | 11 | 1 | 2 | 1 | | | | | 2 | | | | | | | | | |
| **1984** | 15 | 18 | 55 | 35 | 45 | 25 | 16 | 19 | 9 | 7 | 5 | 3 | 2 | 9 | 3 | 8 | | | | | | | | | | |
| **1985** | 16 | 107 | 208 | 147 | 144 | 200 | 109 | 76 | 49 | 57 | 35 | 28 | 20 | 11 | 27 | 7 | 7 | | 3 | | | | | | | |
| **1986** | 18 | 86 | 299 | 221 | 155 | 150 | 235 | 102 | 78 | 49 | 56 | 39 | 28 | 22 | 10 | 22 | 1 | 4 | | 1 | | | | | | |
| **1987** | 11 | 163 | 295 | 276 | 225 | 150 | 141 | 216 | 89 | 80 | 36 | 54 | 27 | 21 | 13 | 8 | 20 | 4 | 3 | | 1 | | | | | |
| **1988** | 41 | 237 | 598 | 367 | 270 | 222 | 168 | 158 | 201 | 104 | 76 | 55 | 54 | 32 | 28 | 13 | 5 | 22 | 2 | 4 | | 1 | | | | |
| **1989** | 31 | 276 | 568 | 581 | 423 | 273 | 232 | 191 | 145 | 175 | 100 | 66 | 34 | 36 | 21 | 11 | 2 | 3 | 17 | 3 | 1 | | 1 | | | |
| **1990** | 5 | 338 | 645 | 518 | 523 | 395 | 251 | 206 | 155 | 118 | 149 | 66 | 46 | 21 | 22 | 13 | 12 | 4 | 1 | 10 | | | | | | |
| **1991** | 7 | 246 | 765 | 600 | 484 | 439 | 339 | 223 | 186 | 136 | 90 | 114 | 59 | 40 | 17 | 20 | 9 | 4 | 2 | 1 | 8 | 1 | | | | |
| **1992** | 9 | 292 | 886 | 598 | 492 | 364 | 322 | 259 | 179 | 142 | 102 | 70 | 70 | 41 | 29 | 11 | 14 | 5 | 3 | 1 | | 6 | | | | |
| **1993** | 9 | 193 | 748 | 559 | 425 | 392 | 286 | 223 | 178 | 119 | 81 | 53 | 36 | 47 | 19 | 12 | 6 | 5 | 6 | | | 1 | 3 | | | |
| **1994** | 13 | 273 | 731 | 680 | 556 | 433 | 389 | 284 | 217 | 147 | 121 | 69 | 47 | 28 | 36 | 15 | 17 | 4 | 4 | 2 | | | | 4 | | |
| **1995** | 14 | 390 | 852 | 557 | 613 | 471 | 375 | 308 | 258 | 164 | 92 | 78 | 43 | 23 | 24 | 19 | 5 | 5 | | 4 | 2 | | | | | |
| **1996** | 33 | 582 | 1053 | 811 | 537 | 533 | 451 | 333 | 273 | 164 | 104 | 79 | 47 | 28 | 16 | 14 | 8 | 5 | 3 | 2 | 1 | | | | | |
| **1997** | 29 | 576 | 1096 | 829 | 665 | 475 | 457 | 351 | 305 | 187 | 148 | 75 | 53 | 25 | 13 | 10 | 12 | 4 | | | | 1 | | | | |
| **1998** | 20 | 614 | 1182 | 1033 | 753 | 615 | 441 | 425 | 349 | 212 | 143 | 119 | 69 | 44 | 17 | 7 | 4 | 4 | 3 | | | | 3 | | | 1 |
| **1999** | | 623 | 1078 | 960 | 952 | 643 | 506 | 367 | 368 | 278 | 196 | 112 | 88 | 45 | 33 | 6 | 1 | 3 | 3 | | | | | | | |
| **2000** | 20 | 586 | 1123 | 885 | 837 | 828 | 515 | 421 | 300 | 284 | 205 | 163 | 84 | 69 | 32 | 19 | 6 | | 1 | 3 | | | | | | |
| **2001** | 16 | 698 | 1333 | 995 | 829 | 735 | 742 | 460 | 356 | 267 | 240 | 196 | 126 | 68 | 51 | 22 | 12 | 1 | 1 | | 3 | | | | | |
| **2002** | 27 | 678 | 1377 | 1050 | 905 | 744 | 646 | 664 | 390 | 277 | 216 | 175 | 146 | 100 | 37 | 40 | 15 | 7 | 3 | | | 1 | | | | |
| **2003** | 18 | 782 | 1458 | 1256 | 1050 | 834 | 684 | 570 | 598 | 293 | 235 | 158 | 116 | 95 | 58 | 21 | 23 | 2 | | 3 | | | | | | |
| **2004** | 63 | 863 | 1582 | 1303 | 1178 | 972 | 745 | 565 | 489 | 438 | 249 | 162 | 97 | 72 | 56 | 25 | 17 | 7 | 2 | | 1 | | | | | |
| **2005** | 105 | 1141 | 1826 | 1510 | 1239 | 1054 | 820 | 648 | 482 | 444 | 315 | 167 | 104 | 73 | 53 | 35 | 30 | 2 | 1 | | | 2 | | | | |
| **2006** | 57 | 1432 | 2340 | 1810 | 1547 | 1252 | 1052 | 843 | 655 | 455 | 415 | 277 | 129 | 93 | 50 | 29 | 22 | 13 | 4 | 1 | | | | | | 1 |
| **2007** | | 19 | 202 | 170 | 144 | 128 | 100 | 87 | 72 | 55 | 41 | 27 | 32 | 13 | 1 | 10 | 5 | 2 | 2 | | | | | | | |

sixteen or more parities gave totals that are by far higher than the numbers of dams with 14 and 15 parities. The percentage of very long-lived productive dams having sixteen or more parities has decreased over time, staring at 1.84% in 1986, 2.08% in 1987 and decreasing steadily to 0.56% in 2006.

Population dynamics were summarized using models originally developed by Leslie (1945; 1948). Equilibrium age-specific vectors for reproduction rate (Mx, x=0 to 14) were:

0.00 0.00 1.00 0.46 0.74 0.76 0.75 0.68 0.77 0.76 0.68 0.75 0.66 0.51 0.11;

and

0.00 0.00 0.00 1.00 0.54 0.68 0.69 0.74 0.61 0.61 0.70 0.68 0.61 0.52 0.26,

for females calving first in their 2nd and 3rd years of life, respectively.
Corresponding, equilibrium age specific vectors for survival (Sx, x=0 to 14) were:

0.57 0.90 0.74 0.91 0.86 0.84 0.84 0.86 0.84 0.81 0.83 0.74 0.51 0.11;

and

0.80 0.90 0.93 0.66 0.81 0.81 0.84 0.82 0.83 0.82 0.77 0.69 0.57 0.27.

It should be noted that reproduction and survival rates are empirical and therefore should be interpreted as such. There were 21% more cows in reproduction and herd size was maintained with a lower proportion of heifer calves (57% vs. 80%) needed as replacements with first calving at 2 years of age rather than 3. This is also confirmed by the higher survival rates to five years of age of the cows calving first at 2 years of age versus cows calving for the first time at three years of age. The surplus heifers could be sold as replacements to a terminal crossbreeding system thereby generating income to the farmer. This system will contribute to sustainability and poverty alleviation.

### *3.3.2 Genetic statistics*

Table 3.7 shows the estimates of generation interval in each year for the four gametic pathways partitioned. Only generation interval values are available for the SS and SD paths from the period 1973 to 1976. These values will not be considered further due to the lack of information for the DS and DD paths. For the most part the generation intervals were more or less constant over time at or just under approximately 6 years. There was no appreciable difference for any of the paths of selection.

Family size refers to the number of offspring of an individual that contribute to the next generation (Falconer and Mackay, 1996). The number of progeny in sire families varied from 1 to 481 with a mean of 34.9 and a variance of 2069.3. The number of progeny in dam families varied from 1 to 30 with a mean of 2.91 and a variance of 5.76. The high dam family size could be attributable to twinning and the fact that embryo transfer is used in the Nguni breed.

**Table 3.6** Generation intervals for the four selection paths (SS = sire to son, SD = sire to daughter, DS = dam to son and DD = dam to daughter) and averages for sire paths (s.), dam paths (d.) and all paths (pop) arrayed by birth year.

| Year | SS | SD | DS | DD | S. | D. | Pop |
|---|---|---|---|---|---|---|---|
| **1973** | 6.18 | 6.09 | | | 6.14 | | |
| **1974** | 7.00 | 7.05 | | | 7.03 | | |
| **1975** | 0.00 | 8.07 | | | 8.07 | | |
| **1976** | 9.12 | 8.94 | | | 9.03 | | |
| **1977** | 0.00 | 9.99 | 2.35 | 4.55 | 9.99 | 3.82 | 6.90 |
| **1978** | 11.03 | 11.07 | | 3.55 | 11.05 | 3.55 | 6.55 |
| **1979** | 0.00 | 7.03 | | 4.71 | 7.03 | 4.71 | 5.74 |
| **1980** | 0.00 | 5.01 | | 5.22 | 5.01 | 5.22 | 5.17 |
| **1981** | 3.73 | 4.64 | 3.53 | 5.92 | 4.46 | 5.70 | 5.31 |
| **1982** | 5.65 | 6.28 | 4.00 | 6.29 | 6.11 | 5.92 | 5.97 |
| **1983** | 4.81 | 5.94 | 5.94 | 5.46 | 5.59 | 5.50 | 5.53 |
| **1984** | 4.99 | 6.03 | 7.64 | 5.06 | 5.63 | 5.63 | 5.63 |
| **1985** | 5.50 | 5.85 | 6.27 | 6.04 | 5.72 | 6.09 | 6.00 |
| **1986** | 5.59 | 5.61 | 6.03 | 6.39 | 5.60 | 6.33 | 6.14 |
| **1987** | 5.85 | 5.75 | 6.78 | 6.48 | 5.78 | 6.53 | 6.31 |
| **1988** | 5.63 | 5.46 | 6.14 | 5.89 | 5.52 | 5.94 | 5.82 |
| **1989** | 5.69 | 5.84 | 6.18 | 6.22 | 5.80 | 6.21 | 6.09 |
| **1990** | 5.35 | 5.44 | 6.33 | 5.85 | 5.42 | 5.92 | 5.78 |
| **1991** | 5.58 | 5.55 | 6.18 | 5.98 | 5.56 | 6.01 | 5.88 |
| **1992** | 5.29 | 5.57 | 5.54 | 5.65 | 5.49 | 5.63 | 5.59 |
| **1993** | 5.30 | 5.50 | 5.62 | 5.85 | 5.45 | 5.82 | 5.72 |
| **1994** | 5.44 | 5.67 | 6.02 | 5.90 | 5.61 | 5.92 | 5.84 |
| **1995** | 5.16 | 5.77 | 6.00 | 5.92 | 5.61 | 5.93 | 5.85 |
| **1996** | 5.69 | 5.62 | 5.80 | 5.48 | 5.64 | 5.53 | 5.56 |
| **1997** | 5.87 | 5.80 | 6.17 | 5.65 | 5.82 | 5.72 | 5.74 |
| **1998** | 5.59 | 5.77 | 5.54 | 5.76 | 5.73 | 5.73 | 5.73 |
| **1999** | 5.57 | 5.91 | 6.10 | 5.97 | 5.84 | 5.98 | 5.95 |
| **2000** | 5.44 | 5.90 | 6.13 | 5.97 | 5.79 | 5.99 | 5.94 |
| **2001** | 6.56 | 6.16 | 6.34 | 6.02 | 6.25 | 6.05 | 6.10 |
| **2002** | 6.49 | 6.13 | 6.38 | 5.94 | 6.22 | 5.99 | 6.04 |
| **2003** | 6.28 | 5.89 | 6.25 | 5.81 | 5.97 | 5.85 | 5.89 |
| **2004** | 5.14 | 6.23 | 4.35 | 6.12 | 5.89 | 5.63 | 5.75 |

Presented in Table 3.8 are minimums, maximums and averages of the generation numbers and inbreeding coefficients for animals recorded in the South African Nguni herdbook. From 1980 onwards some inbred animals were observed as a result of the data that came from state-run experiment stations. There was a slow increase in the numbers of animals with known pedigrees accompanied by a steady increase in inbreeding after the establishment of the South African breed society in 1986. However, the average level of inbreeding has remained low presumably due to the open recording system maintained by the society. The average inbreeding for the 2004 to 2006 subpopulation was 0.0076 and the change in inbreeding ($\Delta F$) was 0.002976. Thus the estimated effective population size was 168 for this period.

### *3.4 Discussion*

In South Africa, like in many emerging countries, the development of agriculture and breeding programs has resulted in serious changes in cattle breeding stocks during the last decades. The establishment of herd book societies in conjunction with intensive breeding activities has led to a pronounced supra-regional propagation of certain cattle breeds due to improvements in performance due to gradual improvement (FAO 1998). The situation is slightly different in South Africa with the Nguni breed of cattle. The breed was bred by the traditional farmers for many years and recently some animals have been acquired by the modern farmers who established a herd book society (Scholtz and Ramsay, 2007).

**Table 3.7** Inbreeding coefficients and generation numbers of animals recorded in the South African Nguni herdbook.

| | Inbreeding | | | Generation Number | | |
|---|---|---|---|---|---|---|
| **Year** | **Average** | **Minimum** | **Maximum** | **Average** | **Minimum** | **Maximum** |
| **1966** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1967** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1968** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1969** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1970** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1971** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1972** | 0.0000 | 0 | 0.0000 | 1.0000 | 1 | 1.00 |
| **1973** | 0.0000 | 0 | 0.0000 | 1.0208 | 1 | 1.50 |
| **1974** | 0.0000 | 0 | 0.0000 | 1.0109 | 1 | 1.50 |
| **1975** | 0.0000 | 0 | 0.0000 | 1.0090 | 1 | 1.50 |
| **1976** | 0.0000 | 0 | 0.0000 | 1.0089 | 1 | 1.50 |
| **1977** | 0.0000 | 0 | 0.0000 | 1.0204 | 1 | 1.75 |
| **1978** | 0.0000 | 0 | 0.0000 | 1.0298 | 1 | 1.75 |
| **1979** | 0.0000 | 0 | 0.0000 | 1.0315 | 1 | 1.75 |
| **1980** | 0.0004 | 0 | 0.1250 | 1.0462 | 1 | 2.62 |
| **1981** | 0.0004 | 0 | 0.0625 | 1.0990 | 1 | 2.62 |
| **1982** | 0.0002 | 0 | 0.1250 | 1.1223 | 1 | 2.50 |
| **1983** | 0.0002 | 0 | 0.0625 | 1.1460 | 1 | 3.00 |
| **1984** | 0.0006 | 0 | 0.2500 | 1.2829 | 1 | 2.81 |
| **1985** | 0.0002 | 0 | 0.2500 | 1.5736 | 1 | 3.12 |
| **1986** | 0.0011 | 0 | 0.2500 | 1.6843 | 1 | 3.28 |
| **1987** | 0.0016 | 0 | 0.2500 | 1.7004 | 1 | 3.34 |
| **1988** | 0.0026 | 0 | 0.2500 | 1.8890 | 1 | 3.56 |
| **1989** | 0.0026 | 0 | 0.2500 | 2.0327 | 1 | 3.84 |
| **1990** | 0.0038 | 0 | 0.3125 | 2.1273 | 1 | 4.47 |
| **1991** | 0.0058 | 0 | 0.3750 | 2.3319 | 1 | 4.56 |
| **1992** | 0.0060 | 0 | 0.3750 | 2.3657 | 1 | 4.66 |
| **1993** | 0.0050 | 0 | 0.3125 | 2.2939 | 1 | 4.69 |
| **1994** | 0.0054 | 0 | 0.3125 | 2.4392 | 1 | 4.94 |
| **1995** | 0.0052 | 0 | 0.2656 | 2.5223 | 1 | 5.20 |
| **1996** | 0.0058 | 0 | 0.3125 | 2.7038 | 1 | 5.47 |
| **1997** | 0.0077 | 0 | 0.3135 | 2.8373 | 1 | 5.59 |
| **1998** | 0.0083 | 0 | 0.2969 | 3.0545 | 1 | 5.59 |
| **1999** | 0.0067 | 0 | 0.3203 | 3.1932 | 1 | 5.66 |
| **2000** | 0.0067 | 0 | 0.2539 | 3.2789 | 2 | 5.95 |
| **2001** | 0.0068 | 0 | 0.3125 | 3.3216 | 1 | 6.00 |
| **2002** | 0.0071 | 0 | 0.3750 | 3.3777 | 1 | 6.22 |
| **2003** | 0.0071 | 0 | 0.3750 | 3.4480 | 2 | 6.44 |
| **2004** | 0.0068 | 0 | 0.2822 | 3.5383 | 2 | 6.49 |
| **2005** | 0.0080 | 0 | 0.2988 | 3.8929 | 2 | 6.79 |
| **2006** | 0.0080 | 0 | 0.3750 | 4.0057 | 2 | 6.83 |
| **2007** | 0.0062 | 0 | 0.2598 | 3.9008 | 2 | 6.57 |

Demographic analysis includes the sets of methods that allow us to measure the dimensions and dynamics of populations. One of the most important dimensions of the population is its growth.  Population growth is a function of birth, mortality, immigration and emigration (Rockwood, 2006).  For the Nguni population recorded by the South African breed society, census numbers have expanded from 48 in 1973 to nearly 12,000 in 2006. This increase has occurred despite the fact that current participation in the national beef cattle performance recording programs is estimated to account for only approximately 27% of Nguni breeders. There appears to be little difference in the age distributions of sires and dams, with many cows achieving 8 or more parities supporting the claim for superior longevity (Scholtz, 1988; The South African Livestock Breeding, 2004). However, the percentage of very long-lived productive dams has decreased over the 20 year period from 1986 to 2006.

Many emerging farmers view their cattle herds as their bank (Bester *et al*., 2003). Thus, the rate at which their herd expands may be viewed as a form of economic interest rate. Here it has been shown that implementing the management practice of joining heifers with a bull at approximately 15 months of age can substantially increase both the number of cows in production and number of calves produced, relative to the common practice of waiting for a cow to attain 3 years of age before having her first calf. Potter *et al.* (1998) also found a greater percentage of cows in a herd were reproducing when heifers were calved first at two as opposed to three years of age. This resulted in more weight being produced and greater production per hectare with first calving at the younger age. These results confirm the earlier observation of

Núñez-Dominguez *et al*. (1991) that calving heifers first at two years increased lifetime production per cow and resulted in greater economic efficiency than calving first at three years of age.

Family size refers to the number of offspring of an individual that become breeding individuals in the next generation (Falconer and Mackay, 1996). Under ideal conditions each parent has an equal chance of contributing offspring to the next generation. In practice, particularly in production animals, genetic contribution of the parents is not the same. Unequal contribution from different families leads to differences or variation in family size. When there is large variation in family size the next generation is made up of the progeny of a smaller than expected number of parents. This can be related to loss of genetic variation through an increased rate of inbreeding (Nomura *et al*., 2001).

The variance of family size can be minimized as the numbers of offspring approach becoming equal for all parents (Falconer and MacKay, 1996). Compared to other studies, the variance of family size in the recorded South African Nguni population is fairly small. Nomura *et al.* (2001) reported that the variance of family size was 41,415 in 1985, 126,963 in 1995 and 132,357 in 1997, for the Japanese Black cattle. This increase of the variance was mainly due to the intensive use of a few popular sires (Nomura *et al*., 2001). It can be speculated that this very large variance of family size made a sizeable contribution to the effective population size of Japanese Black being 17.2 compared to the estimated 168 for South African Nguni.

The annual change in inbreeding observed in the current study was less than the 0.5% suggested by Nicholas (1989) as acceptable and the 1% change per generation that FAO (1998) suggested was minimal for allowing continued genetic gain. The animals in the years closest to date provide insight into $F_x$ in the future generations. The Food and Agriculture Organization (FAO, 2004) has recommended maintaining $N_e$ at 50 to 100 animals per generation. $N_e = 50$ correspond to 1% per generation rate of inbreeding. The $N_e$ reported here is greater than the FAO (1998) recommendation and within the 25 to 255 range of effective population size that was suggested as being critical for maintaining fitness by Meuwissen and Woolliams (1994).

The current estimate of $N_e$ is large compared to other breeds. McParland *et al*. (2007) estimated effective population sizes of 64, 127, and 75 for Irish Herefords, Simmental, and Holstein-Friesian, respectively. Italian beef cattle populations were found to have $N_e$ in the range from 122-138 (Bozzi *et al*., 2006). Estimates of $N_e$ for Danish dairy cattle populations ranged from 49-157 (Sorenson *et al*., 2005). Although the estimated $N_e$ for South African Nguni was a little greater than in the referenced studies, these had more complete pedigree data. However, inbreeding levels are downward biased when pedigree information and effective population size is overestimated when the pedigree is incomplete (Boichard *et al*., 1997).

One issue that needs to be investigated further is the assumption that the migrants are unrelated and not inbred. Violation of this assumption may easily lead to inbreeding depression despite pedigree analysis indicating acceptable levels of $F_x$ and $\Delta F$. In recent years there has been a strong drive within the breed to emphasis a certain type of an animal as the typical Nguni. The favoured animal appears to be of a certain ecotype with other ecotypes being discriminated against. This fad leads to the favoured ecotype been sourced from villages were they occur in substantial numbers. However, in these villages there is normally a dominant bull that sires a disproportionately large number of calves. Further, chances are that a son may take over as a dominate bull. Thus, animals entering the Nguni herdbook may already be inbred, despite the lack of any pedigree information.

The rate of genetic and economic progress in the population of beef producing animals both at farm/breeder and breed level depends on the turnover of breeding stock (i.e., the generation interval), among other things. However, Snelling *et al.* (1995) argue that to be profitable, females remaining in production beyond their breakeven age must compensate for females that are culled earlier in their lives. Improvement of longevity in cattle affects profitability by reducing replacement costs and increasing the proportion of cows producing at mature level (van Arendonk, 1985). Longevity in parental stock will increase the generation interval, but at the same time, increase the accuracy of the predicted breeding value from the additional data (Nwakalor *et al.,* 1986). Unfortunately Rogers *et al*. (2004) found a dearth of indicators expressed early in life that would aide selection for increased longevity. In the current study generation intervals were similar for both males and females presenting an opportunity to increase the rate of genetic progress without adversely affecting profitability by reducing generation intervals along the sire paths of selection. If the goal is to make genetic improvement, generations can be turned-over more rapidly than has been the case with the Nguni.

Nomura *et al*. (2001) reported long generation intervals for Japanese Black cattle, mainly due to the lengthy generation intervals on the sire to progeny selection paths. This was attributed to the widespread use of proven sires.  The Nguni society has a reputation to be the strictest breeding society when selecting bulls, only about 21% of the bulls presented for inspection are selected (Scholtz, Personal communication). Data presented in the current study confirms that bulls selected at 2 years of age are used for several years in the Nguni breed. The average population generation interval was calculated to be 6.09 for this study. This value is greater than the 4.5 to 5 years observed by Dalton (1980) and less than the 9.09 years for Japanese Black cattle (Nomura *et al*., 2001). Koch *et al*., (1994) and MacNeil *et al*., (1998) reported generation intervals for the four selection paths ranging from 3.66 to 5.03 and 2.81 to 4.97 for different selection lines, respectively. These results indicate an opportunity exist to further enhance genetic improvement through reducing generation interval with the Nguni breed.

MacNeil and Matjuda (2007) considered Nguni females as a specialized dam line in a terminal weaner production system both for the emerging and developed beef production sector. However, an appropriate breed structure to implement such a system is not currently in place. Nguni cattle have been depopulated in rural villages by the movement into the hands of stud farmers and dissemination back to these areas is only beginning (Bester *et al*., 2003). Given this need, it is a necessity that the Nguni population grow rapidly. However, the current breed structure does not promote gene flow from the elite breeders through the multipliers to emerging commercial beef producers. It should be noted that use of a terminal sire breed with Nguni females is likely only feasible with first calving at 2 years of age. The results of the Leslie matrix analysis result shows that with first calving at 3 years almost all cows must be bred to Nguni bulls simply to maintain herd size.

### *3.5 Summary and Conclusions*

The Nguni breed of cattle has a great potential for expanding into the diverse markets that exist both within and beyond the boundaries of South Africa. Demographic and genetic analyses indicate that Nguni is in a favourable position to grow from within the current population for some time. An opportunity exists to increase the rate of genetic improvement by shortening the selection paths from sire to descendants. The breed is capable of reducing age of first calving to two years and thereby increasing the number of females in reproduction to the effect of increasing the number of calves produced per year.

Genetic analysis indicate that the breed is in a favourable position to continue countering the undesirable effects of inbreeding as the history show the effective population size and inbreeding levels that are conducive to further healthy population growth. This should encourage the breed to promote the existence of different subclasses in the form of the different ecotypes. The coexistence of the three schools of thought within the breed seems to have been a positive thing as it promoted diversity within the breed. Further investigations need to be carried out to examine the effect of the performance history of the breed. The results obtained in the study and envisioned studies of the history of the performance of the breed are expected to help in forecasting the future of the breed.

# CHAPTER 4

# USING INDEX-IN-RETROSPECT TO EVALUATE PAST SELECTION FOR PERFORMANCE TRAITS IMPOSED ON SOUTH AFRICAN NGUNI CATTLE

### *4.1 Introduction*

The Nguni has performance attributes including high fertility, low maintenance requirements, ease of calving, adaptability, resistance to parasites, resistance to tick-borne diseases, good temperament, longevity, browsing, good walking ability (Scholtz, 1988; South African Livestock Breeding, 2004). Consequently, the breed is viewed as having cost-effective capacity for beef production and the ability to thrive under harsh conditions. These characteristics seemingly position Nguni for use as a specialized dam line, particularly by emerging farmers. Local environment, culture and values of communities of the emerging farmers are reflected in the key traits and/or functions of Nguni cattle (Rege, 2001). The Nguni may be adapted to local environmental stresses, able to provide traction, and produce both meat and milk. Behind these traits are the breeding practices and other indigenous knowledge systems that have been applied for the maintenance of these populations, and the genetic diversity that they represent.

Selection is the primary force for changing average genetic composition of herds and breeds. Selection, which is differential reproduction of phenotypes, can occur at any stage of the life cycle and be due to natural causes or directed by man (Koch *et al.*, 1974). For single trait selection, genetic change is predicted by observed selection differentials multiplied by heritability. However, if multiple traits are involved this simple prediction is not appropriate, as pointed out by Magee (1965). The observed cumulative selection differentials of parents are a function of multiple trait relationships existing in the population over time (Koch *et al*., 1994). Therefore change from selection depends on (1) selection differentials in primary and correlated traits, (2) the fraction of selection differentials due to average genetic differences of parents and (3) interval between selected generations. It is noted that organized selection was absent during the subsistence phase of development. It is assumed that nature and man practiced some selection resulting in the present day Nguni. To gain some understanding of which traits were used by breeders and nature in selection and the emphasis put on them, index-in-retrospect methods were used (Dickerson *et al*., 1954). Therefore, the objective of the current study was to evaluate past selection for performance traits imposed on South African Nguni cattle using index-in-retrospect.

### *4.2 Materials and methods*

Data used in the current study included estimated breeding values (EBV) for animals born during the period 1973 to 2006. These EBV were obtained from an official routine national genetic evaluation of the South African Nguni breed conducted by the Agricultural Research Council (ARC). The data included EBV for birth weight direct ($BWT_d$), birth weight maternal ($BWT_m$), weaning weight direct ($WWT_d$), weaning weight maternal ($WWT_m$), yearling weight (YWT), 18-months weight (18WT), average daily gain (ADG), shoulder height (SDH), scrotal circumference (SCR), body length (LEN), mature weight (MWT) and calf tempo (CT). These data are analyzed by the ARC with a series of multiple trait models (Table 4.1). With the exception of CT, all EBV are expressed on a per animal basis. Calf tempo is expressed per 100 daughters and thus the results obtained from the national evaluation were divided by 100 to express all EBV and results derived from them on a per animal basis.

**Table 4.1** Multiple trait models for the genetic evaluation of Nguni cattle.

| Model | Traits[1] in the Analysis | Estimated Breeding Values[2] reported |
|---|---|---|
| 1 | BWT, WWT | $BWT_d$, $BWT_m$, $WWT_d$, $WWT_m$, |
| 2 | WWT, YWT, 18WT | YWT, 18WT |
| 3 | WWT, MWT | MWT |
| 4 | WWT, ADG, DFI, SDH, SCR, LEN | ADG, DFI, SDH, SCR, LEN |
| 5 | CT | CT |

[1] BWT = birth weight (kg), WWT = weaning weight (kg), YWT = yearling weight (kg), 18WT = 18-month weigh (kg), MWT = mature weight (kg), ADG = average daily gain (g/d), DFI = daily feed intake (kg), SDH = shoulder height (mm), SCR = scrotal circumference (mm), LEN = body length (mm), CT – calf tempo (Number of calves per 100 daughters).
[2] Subscripts d and m denote direct and maternal effects, respectively.

The EBV were used to calculate the genetic selection differentials ($\Delta g_i$) required to determine the weights of an index-in-retrospect. Those animals that subsequently became parents (*i.e.* were selected) were identified and their individual selection differentials were calculated as the difference between their EBV and the average EBV of the population (Van Vleck, 1993). The genetic selection differentials were calculated separately and accumulated over the four selection paths for registered sires and dams. The index-in-retrospect is an index that might have been used for selection to produce gains that have occurred even though the weights for the index might have been unknown at the time of selection (Dickerson *et al.*, 1954). The *index-in-retrospect* is given by:

$$I = \sum w_j EBV_j$$

where I is the underlying unknown index. Letting D be the selection intensity factor, the regression of $EBV_j$ on I will give the expected genetic selection differential for trait j:

$$E\left[\Delta g_j\right] = \frac{Cov\left(g_j, I\right)}{\sigma_I^2}\Delta I = \frac{Cov\left(g_j, I\right)}{\sigma_I}D = \left(\frac{D}{\sigma_I}\right)Cov\left(g_j, I\right)$$

If $D/\sigma_I$ (which is a constant for all the traits in the index) is set to 1, the expected values of the genetic selection differentials are:

$$E\left[\Delta g_1\right] = Cov\left(g_1, I\right) = w_1\sigma_{g_1}^2 + w_2\sigma_{g_1g_2} + \ldots + w_N\sigma_{g_1g_N}$$

$$E\left[\Delta g_2\right] = Cov\left(g_2, I\right) = w_1\sigma_{g_1g_2} + w_2\sigma_{g_2}^2 + \ldots + w_N\sigma_{g_2g_N}$$

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$$E\left[\Delta g_N\right] = Cov\left(g_N, I\right) = w_1\sigma_{g_1g_N} + w_2\sigma_{g_2g_N} + \ldots + w_N\sigma_{g_N}^2$$

The weights for the underlying index ($w_i$) can be estimated by equating the estimated genetic selection differentials to the right hand sides of the above equations as: $w = G^{-1}\Delta g$ (Van Vleck, 1993). It is important to note that the original index in retrospect was developed based on phenotypic changes in performance. It should however be acknowledged that there is no consensus regarding the use of estimated breeding values to derive weights for the index in retrospect. According to Van Vleck (1993) genetic selection differentials could be derived using on difference between estimated breeding values of the parents and progeny. Genetic variance-covariance matrix G should be estimated from ordinary variance component analysis (Yamada, 1977). It is accepted that the use of REML, fitting an animal model that includes a complete relationship matrix and all records of parents is reported to provide unbiased estimates of the base population additive genetic variance (Sorensen and Kennedy, 1984; Bulmer, 1985; Juga and Thompson 1989; Kennedy, 1990). In the current study, genetic variance-covariance matrix (G) (Table 4.2), were those generated by the genetic evaluation section of the ARC using REML. Genetic trends were also estimated from the EBV generated by the ARC. The genetic trend was measured as the regression of yearly mean EBV on generation number.

**Table 4.2** The variance-covariance matrix (G) used to determine the index-in-retrospect weights for the EBV[1,2]

|  | $BW_d$ | $BW_m$ | $WW_d$ | $WW_m$ | YWT | W18 | ADG | HGT | SCR | LEN | MWT | CT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $BW_d$ | 3.74 |  | 10.29 |  |  |  |  |  |  |  |  |  |
| $BW_m$ |  | 1.21 |  | 3.96 |  |  |  |  |  |  |  |  |
| $WW_d$ | 10.29 |  | 63.87 |  | 181. | 229. | 605. | 120. | 55. | 199. | 177. |  |
| $WW_m$ |  | 3.96 |  | 49.17 |  |  |  |  |  |  |  |  |
| YWT |  |  | 181. |  | 261. | 332. |  |  |  |  |  |  |
| W18 |  |  | 229. |  | 332. | 457. |  |  |  |  |  |  |
| ADG |  |  | 605. |  |  |  | 14450. | 1342. | 758. | 1692. |  |  |
| HGT |  |  | 120. |  |  |  | 1342. | 407. | 79. | 369. |  |  |
| SCR |  |  | 55. |  |  |  | 758. | 79. | 280. | 125. |  |  |
| LEN |  |  | 199. |  |  |  | 1692 | 369. | 125. | 501. |  |  |
| MWT |  |  | 177. |  |  |  |  |  |  |  | 950. |  |
| CT |  |  |  |  |  |  |  |  |  |  |  | 0.085 |

[1] BWT = birth weight, WWT = weaning weight, YWT = yearling weight, 18WT = 18-month weight, ADG = average daily gain, DFI = daily feed intake, HGT = shoulder height, SCR = scrotal circumference, LEN = body length, CT – calf tempo.

[2] Subscripts d and m denote direct and maternal effects, respectively.

The formula of Brinks *et al*. (1961) was used in calculating the generation number ($gn_i$) of an individual: $gn_i = 1 + (gn_s + gn_d)/2$ where $gn_s$ and $gn_d$ are the generation numbers of the sire and dam respectively. The base population was defined as the unknown parents of the recorded animals. Thus, generation number of each unknown animal was set to zero.

### *4.3 Results*

Tables 4.3 and 4.4 present the numbers of sires and dams, and their weighted cumulated selection differentials, unweighted cumulated selection differentials, ratios of weighted to unweighted selection differentials, and standardized weighted and unweighted selection differentials, respectively. It appears that relatively little directional selection has been applied for the performance traits having EBV, because the standardized selection differentials are consistently much less than 1 standard deviation (except for calf tempo). Ignoring calf tempo because the EBV for it is not calculated for females, approximately 6.4 times more selection has been applied to males than to females for the traits having EBV. However, the greater magnitude of the ratios of weighted to unweighted selection differential indicates a greater degree of natural selection affecting females as opposed to males.

Shown in Table 4.5 are results from the index-in-retrospect calculations using the weighted and unweighted selection differential for Nguni sires and dams. For sires, the indexes-in-retrospect derived from the weighted and unweighted selection differentials are quite similar (r = 0.96). However for dams, the indexes-in-retrospect derived from the weighted and unweighted selection differentials are somewhat different (r = 0.51). Correlations between sire and dam indexes-in-retrospect derived from weighted and unweighted selection differentials were 0.21 and 0.16, respectively.

**Table 4.3** Number of sires; and cumulative weighted and unweighted selection differentials over generations for traits with estimated breeding values$^{1,2}$ on the observed scale and in standard measure; and the ratio of the weighted to unweighted selection differentials

| | | Weighted Selection Differential | | Unweighted Selection Differential | | |
|---|---|---|---|---|---|---|
| EBV | N | Mean | Standardized | Mean | Standardized | Ratio |
| $BW_d$ | 1145 | -0.154 | -0.080 | -0.081 | -0.042 | 1.91 |
| $BW_m$ | 1145 | -0.009 | -0.008 | 0.003 | 0.003 | -2.92 |
| $WW_d$ | 1145 | 0.304 | 0.026 | 0.209 | 0.018 | 1.46 |
| $WW_m$ | 1145 | -0.084 | -0.012 | 0.022 | 0.003 | -3.76 |
| YWT | 1145 | 1.113 | 0.069 | 0.666 | 0.041 | 1.67 |
| W18 | 1145 | 1.356 | 0.063 | 0.806 | 0.038 | 1.68 |
| ADG | 1145 | 1.691 | 0.014 | 1.780 | 0.015 | 0.95 |
| HGT | 1145 | -0.743 | -0.037 | -0.266 | 0.013 | 2.79 |
| SCR | 1145 | 0.287 | 0.017 | 0.403 | 0.024 | 0.71 |
| LEN | 1145 | 0.031 | 0.001 | 0.355 | 0.016 | 0.09 |
| MWT | 1145 | 1.040 | 0.034 | 0.738 | 0.024 | 1.41 |
| CT | 1145 | 0.002 | 0.007 | 0.001 | 0.004 | 1.80 |

[1] BWT = birth weight, WWT = weaning weight, YWT = yearling weight, 18WT = 18-month weight, ADG = average daily gain, DFI = daily feed intake, HGT = shoulder height, SCR = scrotal circumference, LEN = body length, CT = calf tempo. Standardisation was based on additive genetic standard deviation given in Table 4.2.

[2] Subscripts d and m denote direct and maternal effects, respectively.

**Table 4.4** Number of dams, and cumulative weighted and unweighted selection differentials over generations for traits with estimated breeding values$^{1,2}$ on the observed scale and in standard measure; and the ratio of the weighted to unweighted selection differentials.

| | | Weighted Selection Differential | | Unweighted Selection Differential | | |
|---|---|---|---|---|---|---|
| EBV | N | Mean | Standardized | Mean | Standardized | Ratio |
| $BW_d$ | 13712 | 0.010 | 0.005 | 0.017 | 0.009 | 0.75 |
| $BW_m$ | 13712 | -0.004 | -0.004 | 0.001 | 0.001 | -4.19 |
| $WW_d$ | 13712 | 0.209 | 0.018 | 0.113 | 0.010 | 1.86 |
| $WW_m$ | 13712 | 0.024 | 0.003 | 0.009 | 0.001 | 2.65 |
| YWT | 13712 | 0.143 | 0.009 | -0.004 | -0.000 | -35.75 |
| W18 | 13712 | 0.195 | 0.009 | -0.003 | -0.001 | -8.64 |
| ADG | 13712 | 0.394 | 0.003 | -0.225 | -0.002 | -1.74 |
| HGT | 13712 | 0.118 | 0.006 | -0.062 | -0.003 | -1.90 |
| SCR | 13712 | 0.098 | 0.006 | -0.016 | -0.001 | -6.16 |
| LEN | 13712 | 0.219 | 0.010 | 0.126 | 0.006 | 1.74 |
| MWT | 13712 | 0.229 | 0.007 | 0.088 | 0.003 | 2.58 |
| CT[3] | 13712 | 0 | 0 | 0 | 0 | |

[1] BWT = birth weight, WWT = weaning weight, YWT = yearling weight, 18WT = 18-month weight, ADG = average daily gain, DFI = daily feed intake, SDH = shoulder height, SCR = scrotal circumference, LEN = body length, CT – calf tempo.

[2] Subscripts d and m denote direct and maternal effects, respectively.

[3] The calf tempo EBV is not calculated for females.

**Table 4.5** Indexes calculated in retrospect from the weighted and unweighted selection differentials for Nguni sires and dams.

| | Weighted Selection Differential | | Unweighted Selection Differential | |
|---|---|---|---|---|
| EBV[1,2] | Sires | Dams | Sires | Dams |
| $BW_d$ | -0.0464 | 0.00190 | -0.0271 | 0.00415 |
| $BW_m$ | -0.0025 | -0.00666 | 0.0014 | 0.00031 |
| $WW_d$ | 0.0019 | 0.00028 | 0.0020 | 0.00014 |
| $WW_m$ | -0.0015 | 0.00102 | 0.0003 | 0.00016 |
| YWT | 0.0051 | -0.00014 | 0.0026 | -0.00020 |
| W18 | -0.0017 | 0.00039 | -0.0011 | 0.00007 |
| ADG | 0.0002 | -0.00004 | 0.0001 | -0.00006 |
| HGT | -0.0054 | -0.00021 | -0.0035 | -0.00110 |
| SCR | 0.0005 | 0.00022 | 0.0009 | -0.00018 |
| LEN | 0.0024 | 0.00058 | 0.0020 | 0.00123 |
| MWT | 0.0007 | 0.00019 | 0.0004 | 0.00007 |
| CT[3] | 0.0235 | NA | 0.0118 | NA |

[1] BWT = birth weight, WWT = weaning weight, YWT = yearling weight, 18WT = 18-month weight, ADG = average daily gain, DFI = daily feed intake, SDH = shoulder height, SCR = scrotal circumference, LEN = body length, CT – calf tempo.
[2] Subscripts d and m denote direct and maternal effects, respectively.
[3] The calf tempo EBV is not calculated for females.

Genetic trends for recorded performance traits, calculated as the regression of yearly mean EBV on generation number, are presented in Table 4.6. From a biological perspective, the trends are consistently small, across all traits.

**Table 4.6** Genetic trend (change per year) in recorded performance traits of Nguni cattle.

| Trait | Regression coefficient | Standard error |
|---|---|---|
| $BW_d$ | -0.007 | 0.003 |
| $BW_m$ | -0.020 | 0.001 |
| $WW_d$ | 0.389 | 0.010 |
| $WW_m$ | 0.036 | 0.007 |
| YWT | 1.073 | 0.021 |
| W18 | 1.404 | 0.027 |
| ADG | 3.629 | 0.072 |
| HGT | 0.050 | 0.022 |
| SCR | 0.473 | 0.013 |
| LEN | 0.481 | 0.026 |
| MWT | 1.062 | 0.031 |
| $CT^3$ | 0.037 | 0.001 |

[1] BWT = birth weight, WWT = weaning weight, YWT = yearling weight, 18WT = 18-month weight, ADG = average daily gain, DFI = daily feed intake, SDH = shoulder height, SCR = scrotal circumference, LEN = body length, CT – calf tempo.

[2] Subscripts d and m denote direct and maternal effects, respectively.

## *4.4 Discussion*

### *4.4.1 Selection Applied*

Overall the cumulative selection differentials tend to be small and with no clear direction. Mrode (1988) attributed the inability to achieve large differentials to unsoundness, selection on colour, death before production of any offspring and failure to conceive as heifers. In an evaluation of a national recording scheme with many contributing breeders, the lack of a unified breeding objective would also result in reduced selection differentials for the population. To the extent that there is any notable trend in the unweighted selection differentials, it would seem to suggest breeders favor larger males, but small and early maturing females.

Comparison of the weighted and unweighted selection differentials provide insight into joint effects of natural and deliberate or intended selection. Their ratio gives an indication of the effect of natural or deliberate selection on fertility of sires and dams in a population. Larger ratios (ratio > 1.0) indicate that animals with greater EBV have more progeny, with the magnitude of the ratio indicating the relative strength of natural versus imposed selection (Koch *et al*., 1994). Negative ratios indicate selection practices that are opposed to natural selection.

For sires, ratios of weighted to unweighted selection differentials for most traits indicated some harmony between the selection imposed by the breeders and natural selection. Fluctuation of the ratios across traits is interpreted to reflect differing relative emphasis resulting from imposed and natural selection, but not conflicting goals with respect to the recorded EBV.

For dams, breeder preference for small early maturing females seems opposed by natural selection. The weighted selection differentials, which take into account number of progeny, were consistently small and positive. The unweighted selection differentials were positive for early growth and negative for post-weaning traits, reflecting breeder preference. The positive unweighted selection differential for mature weight may reflect a lack of consistency in breeder implementation of their selection objective. Similar to the weighted selection differentials for sires, the weighted selection differentials for dams were almost always positive.

Both birth weight and weaning weight are affected by direct (due to genes of the progeny) and maternal effects (due to genes of the dam). The selection differentials for maternal effects are consistently smaller than those for direct effects, despite the equality of units of expression.

Because the weighted selection differentials for birth weight are consistently less than the unweighted values, natural selection appears to favor lighter birth weights. At a phenotypic level, increases in birth weight generally have been associated with increases in calving difficulty and reductions in calf survival (Bellows *et al*., 1971; Notter, 1978; Nelson and Beavers, 1982). Birth weight has also been shown to be more strongly influenced by variation in direct than by maternal genetic effects (Koch *et al*., 1994). MacNeil *et al*. (1998) eliminated the direct genetic increase in birth weight by selecting for below-average birth weight and maximal yearling weight using mass selection while maintaining positive, albeit reduced genetic increase in yearling weight.

Greater direct effects on weaning weight were consistently favored by selection in this study. However, the observation that sires whose daughters give less milk seem favored by natural selection, but dams that give more milk also leave more progeny poses an interesting conflict. This conflict may, in part, be due to the existence of an antagonism of direct and maternal effects for pre-weaning growth (Koch *et al.,* 1974; MacNeil *et al.,* 1984).

### *4.4.2 Correlations among indexes*

The sire and dam index-in-retrospect weights observed here were very close to zero and generally smaller than those resulting from the selection experiment summarized by Koch *et al*. (1974). The present result implies there has been little consistent directional selection applied by Nguni breeders for the traits recorded, as discussed above.

The correlations between the indexes derived from the weighted and unweighted selection differentials were positive for both sires and dams indicating that selection applied was similar whether differential reproduction was accounted for or not. The only moderate correlation among the indexes-in-retrospect for dams seemingly indicates less consistency in emphasis in the goals of breeders and nature.

Selection criteria for males were almost entirely independent of those used for females. As observed above, if index-in-retrospect weights derived from the unweighted selection differentials were positive for sires then the corresponding index weights were negative for 73% of the EBV in the index-in-retrospect for dams. This causes the correlation between these indexes to be low. This result is interpreted to suggest breeders have conflicting goals for selecting bulls and heifers. These inconsistent goals compromise genetic improvement of the Nguni breed. Thus, there does not seem to be any clear directive as to the breeding objective to be employed for the Nguni breed to reach its potential as a hardy dam as envisioned by Scholtz (1988) and MacNeil and Matjuda (2007) among others.

The lack of clarity as to the emphasis to place on measured traits for selection among males and selection among females may cause breeders to base their main selection on visual appraisal alone (Mrode, 1988). Some of the traits assessed by visual appraisal may be correlated to the traits analyzed in the index-in-retrospect (Roff, 1997). Two such characteristics in selecting animals in the Nguni breed are “thick bulls” for bull selection and “dairy wedge” for females; two characteristics seem to be borne out of the sexual dimorphism theory (Lande, 1980). However functionally related morphological traits are typically genetically correlated with each other to a higher degree than are functionally unrelated traits (Lynch and Walsh, 1998). The divergent selection between the sexes reported in the current study, seems to be geared towards the production of superior bulls to be used as terminal sires instead of superior bulls to produce hardy, fertile replacement animals (Roughsedge *et al*., 2005). However, the high relative importance of maternal traits compared to terminal sire traits, when the goal is to produce herd replacements is demonstrated by Phocas *et al*. (1998).

“Thick bulls” seem to be indicating the muscle development in the bull. Koch and colleagues selected for an analogous trait referred to as muscle score for the period 1974 to 1994 (Koch *et al*., 1994). Muscle score was intended to be a measure of thickness of forearm, loin, rump, and round; presumably a measure of carcass merit. Muscle score like the bull score card used in the Nguni, was assigned at the end of the post-weaning period by a committee (of inspectors in the Nguni) of two to three people.

Several papers and reviews have described negatively correlated responses on reproduction of cows selected for growth rate (Barlow, 1978; Scholtz and Roux, 1984; Luesakul-Reodecha *et al*., 1986). However, recent studies involving both experimental selection data (Mrode *et al*., 1990; Morris *et al*., 1992; Archer *et al*., 1998a) and field data (Meyer *et al*., 1991; Mercadante *et al*., 2003) have refuted this antagonism, indicating that selection of young animals based on body weights did not significantly affect the reproductive performance of cows. An examination of lifetime cow fertility showed that cows with high pre-weaning growth reared more calves to weaning, had less neonatal mortality and also calved earlier than cows with low pre-weaning growth, leading to the conclusion that cows with high pre-weaning growth have improved lifetime fertility (Burrow *et al*., 1991). Archer *et al.* (1998b) reported that results from an experiment with Angus females showed that reproductive performance of females selected for high growth rate was similar to that of females where no deliberate selection pressure was applied whereas females selected for low growth rate had significantly poorer reproductive performance than unselected females and females selected for high growth rate. There is evidence supporting a strong positive relationship between male and female reproduction (Brinks *et al*., 1978; MacKinnon *et al*., 1990; Meyer *et al*., 1991).

### *4.4.3 Genetic trends*

Genetic trends of estimated breeding values for direct and maternal effects were very small but in some instances comparable to trends observed for another South African indigenous breed in the region, the Afrikaner (Beffa *et al.* 2009c). The study of Beffa *et al*. (2009a,b,c,d) was conducted as a selection experiment at an experimental station in Zimbabwe and had several challenges in implementation as result of the environment in which the work was conducted. Data used here were from the field and any selection response across the data set would have resulted from a unified breeding objective being implemented by the breeders. The lack of substantial consistent genetic trends again highlights the lack of any consensus breeding objective for Nguni in South Africa.

## *4.5 Summary and Conclusions*

In a quest to produce a hardy and fertile breed, Nguni seedstock producers should be aware of the inconsistencies in their emphases in selection so as not to limit genetic improvement. Through 2006, there had been little or no selection applied to recorded performance measures, resulting in very small amounts of genetic trend. Also compromising any potential for response to selection was a lack of consistency in selection applied to males and females. For males, selection by breeders was largely consistent with natural selection. However, the imposed and natural selection of females was less consistent. The lack of genetic trend observed in the current study suggests that the Nguni breed is still in the subsistence phase of production.

# CHAPTER 5

# DEVELOPMENT OF BREEDING OBJECTIVES FOR NGUNI CATTLE REFLECTIVE OF THE PRODUCTION, PROFITABILITY AND SUSTAINABLE PHASES OF PRODUCTION

## *5.1 Introduction*

The Nguni has long been promoted as a maternal breed. Breeding work in a beef herd involves breeding for fertility, growth and carcass traits. The problem of choosing which individuals become parents is inherent in beef production. The end products such as, replacement heifers or feeder steers, dictate which group of traits to include in a selection program. Therefore, much of the science and practice of genetic improvement has focused on tools for effecting genetic improvement of individual traits.

The critical question of what exactly constitutes improvement, as opposed to change, has received relatively less attention (MacNeil *et al*., 1997). In pursuit of genetic improvement, an obvious, though far from trivial question in defining objectives of genetic improvement is the identification of the relative economic values of all possible traits that might be improved. However, while James (1982) suggests that the breeder's most important decision is his choice of the objective, he further cautions that a highly efficient selection for the wrong objective may be worse than no selection at all. Existence of industry – wide specifications for beef products, production systems and therefore different enterprises do not suggest that there should be industry-wide selection index. Resources available for production and level of production vary among production systems and units resulting in different economic structures. As a result, relative economic values will differ among production systems and units and each may have different selection index. It is unlikely that there will be a "one size fits all" solution to the problem of selecting breeding stock to maximize profit. However, where there is agreement on the direction/general purpose (maternal) of a breed like a Nguni, direction could be set. The direction is captured in a breeding objective. The primary objective of the current study was to develop a breeding objective for a straight-bred Nguni production system typical of communal and emerging sector of the South African livestock industry. The secondary objective was to ascertain the consistency of breeding objectives reflective of the different phases of agricultural development (i.e. production, productivity, and sustainability phases).

## *5.2 Materials and methods*

### *5.2.1 Simulation model*

A life-cycle simulation (Appendix) starting with 1000 Nguni heifer calves at weaning was used to calculate breeding objectives applicable to an integrated production system using Nguni cattle. The simulation was constructed at the whole animal level and included, continuous time-dependent processes, events, and both stochastic and deterministic elements. Parameters of the simulation were based on phenotypic data gathered in the South African National Beef Cattle Improvement Scheme.

The mental model of the simulated system can be described as follows. At time (yr) 0.0, the simulation was initiated with 1000 weaned heifer calves. These heifer calves may be thought of as a group of “replacement” females. Expense and income were accumulated over the life-cycle of this set of females. Sources of income are sale of females culled for infertility, sale of progenies marketed as beef carcasses after feedlot feeding, and sales of any surviving cows at time = 12.0 upon termination of the simulation. Sources of expense are harvested and grazed feeds consumed by the cows and their progeny, and fixed per head costs associated with each female and each feedlot fed progeny. Life-cycle profitability was calculated at the conclusion of the simulation as the difference between total income and total expense discounted to t=0.

The following general model was used to simulate mean performance for maternally influenced trait (Dickerson, 1969):

$$P = \mu + a_d + a_m$$

where P = level of phenotypic performance, μ = constant base level of performance, $a_d$ = direct genetic effect of Nguni on performance, and $a_m$ = maternal genetic effect of Nguni on performance. For non-maternally influenced traits, the $a_m$ term was dropped from the model.

Weight for Nguni females were simulated from their average growth curve as fitted to data from the South African National Beef Cattle Improvement Scheme. Specifically, the growth curve was derived using individual weight measurements taken at birth, weaning, yearling, 18-months and maturity.

Simulated milk production assumed proportionality of Hereford and Nguni maternal effects on weaning weight from the South African National Beef Cattle Improvement Scheme and level of milk produced by Hereford cows (1062 kg/lactation) as measured by MacNeil and Mott (2000). The simulated milk production of cows < 5 yr old was adjusted relative that of mature cows following the Guidelines for Uniform Beef Improvement Programs age of dam correction factors for weaning weight (Guidelines For Uniform Beef Improvement Programs, 2010).

Feed intake often represents the single greatest cost of beef production (Ferrell and Jenkins, 1984). In this simulation, feed intake of the cows was simulated as a continuous deterministic process occurring over the lifetime of each female following Anderson *et al.* (1983) who modeled feed intake as a function of weight, weight change, and milk production. Feed intake of the feedlot fed progenies was derived from data collected on animals that participated in the centralised growth test (Phase C) of the South African National Beef Cattle Improvement Scheme.

The original females were first exposed for breeding at t ≈ 0.6 and thus, provided they conceive, expected to calve at 2 years of age. Success or failure to conceive was simulated as a stochastic event from the binomial distribution. In the simulation, it was assumed that females that conceive will also calve.  An overall probability (p) of conception (and calving) can be approximated from the inter-calving period reported in the South African National Beef Cattle Improvement Scheme from the equation:

$$ICP = 365p + 730(1 - p)$$

or

$$p = \frac{(730 - ICP)}{365}$$

This formula assumes any simulated female will calve in at least alternate years and thus may be a presumably slight over-estimate of the true probability of conception if less fertile females were also considered. Equivalently, the inter-calving period of the simulated females is constrained to the interval 365 to 730 in accordance with the then minimum breed standards for reproduction in the Nguni breed.

Calf survival was simulated as a stochastic process, with mean level determined from the difference between the probability of conception and calving as shown above and the weaning rate. Weaning weight was simulated as having mean level equal to that observed in the South African National Beef Cattle Improvement Scheme.

At weaning the calves produced were divided into two groups: replacement females and those entering the feedlot. The replacement female group represents an opportunity cost of production and was not considered further. Those entering the feedlot were fed to a breed-specific pseudo-optimal endpoint established to avoid selling their carcasses at a discounted price based on fat depth and/or weight.

The feedlot component of the production system was simulated as having two phases. The first phase is a 28-d adaptation period during which a ration of moderate energy was fed. This phase is followed by a longer second phase (127-d) during which a ration of greater energy density is fed and feed conversion decreased. Data presented by

Strydom *et al*. (2001) was used to benchmark the phenotypes simulated during the feedlot phase and at harvest.

Beef carcasses were the end-product of the simulated production system. Carcass weight and fat depth were simulated stochastically from a bi-variate normal distribution, given their respective deterministically simulated means and coefficients of variation and correlation taken from the literature. Carcasses were valued based on a series of discounts to the base price for carcass weight. Discounts were applied to carcasses that weigh less than 185 kg, carcasses that weigh more than 245 kg, carcasses with fat depth less than 1 mm, carcasses with fat depth between 5 and 10 mm, and carcasses with fat depth greater than 10 mm.

### *5.2.2 Breeding objectives and genetic correlation among objectives*

Three breeding objectives defined as income, profit and economic efficiency were derived in the current study to determine whether the objectives were consistent during the production, productivity/profitability and sustainability phases of agricultural development. The respective breeding objectives for the three phases were defined as income, profit and ratio of income to expense.

The genetic correlation ($r_A$) between breeding objectives was calculated as follows (James, 1982):

$$r_A = \frac{v_1' G v_2}{\sqrt{v_1' G v_1 . v_2' G v_2}}$$

where $v_i$ is a vector of relative economic values for the $i^{th}$ breeding objective, and G is a variance-covariance matrix among traits in the breeding objective (Table 5.1).

### *5.2.3 Calculation of relative economic values and derivation of associated selection criterion*

Income and expense arising as described above were discounted to time = 0 and accumulated for the entire simulation. Profit was then calculated as the difference between the accumulated discounted income and expense. Relative economic values that make up the breeding objective (i.e., production, productivity and sustainability) were calculated by comparison of output (i.e. income, profit or ratio of income to expenses) arising from a base simulation and a similar simulation in which the phenotype for one trait was perturbed by a single unit. Economic values were multiplied by their respective genetic standard deviation in order to provide an indication of their magnitude relative to the expected genetic variation. These values were then divided by the corresponding value for weaning weight to calculate the relative economic values.

**Table 5.1** Genetic variances (on diagonal), covariances (above diagonal) and correlations (below diagonal) among traits in the breeding objective.

| Breeding objective trait | BWT | WWT$_m$ | WWT$_d$ | ADG | FCR | DP | FD | MWT | HP | PR | FR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Birth Weight, kg | 3.740 | 0.000 | 11.410 | 0.682 | -0.418 | 0.000 | -0.021 | 39.934 | 0.000 | 0.000 | 0.000 |
| Milk production, kg | 0.000 | 40.577 | 0.000 | 0.154 | 0.000 | 0.000 | 0.000 | -33.375 | 0.000 | 0.000 | 0.000 |
| Weaning weight, kg | 0.738 | 0.000 | 63.840 | 0.686 | -1.878 | -2.397 | 0.077 | 177.000 | 0.575 | 0.000 | 0.000 |
| Post-weaning ADG, kg/d | 0.290 | 0.110 | 0.390 | 0.048 | -0.069 | 0.021 | 0.006 | 2.373 | 0.000 | 0.000 | 0.000 |
| Feed conversion ratio | -0.460 | 0.000 | -0.500 | -0.670 | 0.221 | 0.059 | 0.000 | -2.173 | 0.000 | 0.000 | 0.000 |
| Dressing percentage, % | 0.000 | 0.000 | -0.500 | 0.160 | 0.210 | 0.360 | 0.005 | 0.000 | 0.000 | 0.000 | 0.000 |
| Fat depth, mm | -0.210 | 0.000 | 0.190 | 0.530 | 0.000 | 0.150 | 0.003 | 0.000 | 0.000 | 0.000 | 0.000 |
| Mature weight, kg | 0.670 | -0.170 | 0.719 | 0.350 | -0.150 | 0.000 | 0.000 | 949.872 | 0.000 | 0.000 | 0.000 |
| Heifer pregnancy, % | 0.000 | 0.000 | 0.180 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.160 | 0.000 | 0.000 |
| Pregnancy rate, % | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | 0.000 |
| Female survival, % | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 2.993 |

### *5.3 Results*

The results of the simulation model including total turnover from each simulation run and relative economic values for different breeding objectives are presented in Table 5.2. Results for the production phase are simulated incomes. Results for the profitability phase are simulated differences between income and expense. Results for the sustainability phase, reflecting production efficiency, are ratios of income over expense. All measures of income and expense were discounted to time 0; the time when the simulated weaned heifer calves entered the system. The economic values reflect differences between the simulations in which an individual phenotype was perturbed by a single unit and the base simulation. Relative economic values were the product of the economic values and the respective genetic standard deviations for the traits. These products were rescaled such that the relative economic value of weaning weight (direct) was fixed at 1.0 across the three breeding objectives. For the ratio traits: feed conversion ratio reflects a change in the ratio with ADG held constant, and hence a perturbation of feed intake; and dressing percentage reflects a change in the ratio with live animal growth held constant, and hence a change in carcass weight.

Correlations among breeding objectives were: 0.92 for the production and profitability objectives, 0.84 for the production and sustainability objectives, and 0.84 for the profitability and sustainability objectives.

**Table 5.2** Relative economic values for traits in the breeding objectives for production, productivity and sustainability.

| Trait | Genetic STD | System output (Rand) | | | Economic values (Rand) | | | Relative economic values, relative to weaning weight | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | PROD | PROF | SUST | PROD | PROF | SUST | PROD | PROF | SUST |
| Base | | 14600.7 | 720.00 | 1.0519 | | | | | | |
| Birth Weight, kg | 1.93 | 14479.9 | 688.40 | 1.0499 | -120.80 | -31.60 | -0.0020 | -0.87 | -0.39 | -0.69 |
| Milk production, kg | 6.37 | 14634.2 | 731.00 | 1.0526 | 33.50 | 11.00 | 0.0007 | 0.80 | 0.45 | 0.80 |
| Weaning weight, kg | 7.99 | 14634.2 | 739.50 | 1.0526 | 33.50 | 19.50 | 0.0007 | 1.00 | 1.00 | 1.00 |
| Post-weaning ADG, kg/d | 0.22 | 15137.9 | 980.30 | 1.069 | 537.20 | 260.30 | 0.0171 | 0.44 | 0.37 | 0.67 |
| Feed conversion ratio | 0.47 | 14600.7 | 648.70 | 1.0465 | 0.0 | -71.30 | -0.0054 | 0.00 | -0.22 | -0.45 |
| Dressing percentage, % | 0.60 | 14845.9 | 965.30 | 1.0695 | 245.20 | 245.20 | 0.0176 | 0.55 | 0.94 | 1.89 |
| Fat depth, mm | 0.051 | 14832.6 | 951.90 | 1.0686 | -47.50 | -47.50 | -0.0109 | 0.04 | 0.08 | 0.15 |
| Mature weight, kg | 30.82 | 14608.4 | 724.60 | 1.0522 | 7.70 | 4.60 | 0.0030 | 0.89 | 0.91 | 1.65 |
| Heifer pregnancy, % | 0.40 | 14702.7 | 763.00 | 1.0547 | 102.00 | 43.00 | 0.0028 | 0.15 | 0.11 | 0.20 |
| Pregnancy rate, % | 0.14 | 14895.8 | 678.60 | 1.0477 | 295.10 | -41.40 | -0.0042 | 0.16 | -0.04 | -0.11 |
| Female survival, % | 1.73 | 14666.8 | 804.20 | 1.0581 | 66.10 | 84.20 | 0.0062 | 0.43 | 0.94 | 1.92 |

### *5.4 Discussion*

The perspective taken here is that of a general purpose, self replacing herd of Nguni cattle that are adapted to the harsh environment of Southern Africa. The breed evolved through a subsistence phase during which there was no directional selection pressure applied to performance traits. However, in meeting national goals for alleviating poverty and reducing hunger (Department of Agriculture – Republic of South Africa, 2008) formal definition of breeding objectives should guide future selection practices. The uniqueness of the South African beef production scenario is that there are commercial farms in the profitability phase and there is ongoing discussion of sustainable production practices, while emerging and communal farmers that have just recently been established on redistributed land are largely in the production phase. In addition, there continues to be a portion of breeders who advocate for breeding Nguni cattle under natural selection alone.

To achieve the breeding goals of the production, profitability and sustainability phases of development, continued selection pressure will be required to improve performance attributes of Nguni cattle. This is achieved through the balancing of breeding values for growth, carcase and fertility as indicated by the economic values for each trait (Table 5.2). In general, the breeding objective for the production phase places greatest emphasis on growth traits *viz.* direct and maternal (milk production) weaning weight, mature weight and carcass weight as manifest through dressing percentage. Fertility and carcass traits received less emphasis. In the breeding objective for the profitability phase, the weaning, carcass and mature weights remained important, with female survival or longevity having increased emphasis. In the breeding objectives for both the production and profitability phases, direct effects on weaning weight were the single most important trait. However, the relative importance of direct effects on weaning weight was reduced relative to carcass weight and female survival in the breeding objective for the sustainability phase.

It is interesting to observe that while successful reproduction is the single most important phenotypic driver of profitable and efficient beef production (Ponzoni and Newman, 1989; Melton, 1995), the pregnancy rates of both heifers and cows received relatively little emphasis in the breeding objectives. In the case of heifer pregnancy, this resulted from relatively few expressions (once per life-cycle per female) and the low genetic variance. The number of expressions of pregnancy rate is greater for cows, however, its genetic variance is even less.

Robertson (1959) suggested a genetic correlation above 0.8 for a trait measured in two environments indicated the lack of genotype by environment interaction. Here, this rule is adopted to evaluate the similarity of breeding objectives (traits) across production phases (environments). The correlations amongst the breeding objectives of the three phases that were estimated here indicate that the three breeding objectives are geared for breeding in the same general direction. It should be borne in mind that modelling of the production system was done at a farm level in the current study. It might be worthwhile in future to investigate the magnitude of the correlation between breeding objectives when modelling is done at levels higher than the farm. However, these breeding goals all imply application of directional selection pressure, with the consequence of their being uncorrelated with the breeding goal under the subsistence phase when (by definition) no directional selection pressure was applied for any of the recorded performance traits.

### *5.5 Summary and Conclusions*

Breeding objectives were developed for the production, profitability, and sustainability phases of development. Emphasis placed on growth traits tended to diminish and emphasis placed on female survival increased with progression through the phases. However, the three breeding objectives were highly correlated and would be expected to move the breed in the same general direction. Therefore producers, irrespective of where they view themselves as being positioned relative to the three phases of production, could contribute to the breeding of Nguni cattle.

# CHAPTER 6

# CONCLUSIONS AND RECOMMENDATIONS

Demographic and genetic analyses indicate that South African Nguni is in a favourable position to grow from within the current population for some time. Opportunities exist to increase the rate of genetic improvement by shortening the selection paths from sire to descendants. The breed is capable of reducing age of first calving to two years and thereby increasing the number of females in reproduction to the effect of increasing the number of calves produced per year.

The breed is in a favourable position to continue countering undesirable effects of inbreeding as the effective population size and inbreeding levels are high and low, respectively. This should encourage the breed to promote the existence of different subclasses in the form of different ecotypes. Coexistence of the three schools of thought within the breed appears to be positive as it has promoted diversity within the breed. Further investigations need to be carried out to examine the effect of the performance history of the breed. The results obtained in the study and envisioned studies of the history of the performance of the breed are expected to help in forecasting the future of the breed.

In a quest to produce a hardy and fertile breed, Nguni seedstock producers should be aware of the inconsistencies in their emphases in selection so as not to limit genetic improvement. Through 2006, there had been little or no selection applied to recorded performance measures, resulting in very small amounts of genetic trend. Also compromising any potential for response to selection was a lack of consistency in selection applied to males and females. For males, selection by breeders was largely consistent with natural selection. However, the imposed and natural selection of females was less consistent.

Breeding objectives were developed for the production, profitability, and sustainability phases of development. Emphasis placed on growth traits tended to diminish and emphasis placed on female survival increased with progression through the phases. However, the three breeding objectives were highly correlated and would be expected to move the breed in the same general direction. Therefore producers, irrespective of where they view themselves as being positioned relative to the three phases of production, could contribute to the breeding of Nguni cattle. Incorporation of these breeding objectives in the national cattle evaluation system may enhance their use by farmers. These results can help subsistence and emerging farmers increase the production of their herds with resulting greater profitability

# REFERENCES

AMER, P. R., and G. C. FOX. 1992. Estimation of economic weights in genetic improvement using neoclassical production theory: an alternative to rescaling. *Animal Production* 54:341-350.

ANDERSON, V. L., JOST, L., DINKEL, C. A., and M. A. BROWN. 1983. Prediction of daily total digestible nutrient requirements of beef cows in northern climates. *Journal of Animal Science* 57:373-386.

APIOLAZA, L. A., and D. J. GARRICK. 2001. Breeding objectives for three silvicultural regimes of radiate pine*. Canadian Journal of Forest Research* 31:654-662.

ARCHER, J. A., ARTHUR, P. F., PARNELL, P. F., and R. J. VAN DE VEN. 1998a. Effect of divergent selection for yearling growth rate on female reproductive performance in Angus cattle. *Livestock Production Science* 57:33-40.

ARCHER, J. A., HERD, R. M., ARTHUR, P. F., and P. F. PARNELL. 1998b. Correlated responses in rate of maturation and mature size of cows and steers to divergent selection for yearling growth in Angus cattle. *Livestock Production Science* 54:183-192.

BARLOW, R. 1978. Biological ramifications of selection for pre-weaning growth in cattle: A review. *Animal Breeding Abstracts* 46:469-494.

BAWDEN, R. J. 1989. Towards action researching systems. In: O. Zuber-Skeritt (Ed.) Action Research for Change and Development. Pp 20−51. Centre for the Advancement of Learning and Teaching, Griffith University, Brisbane, Australia.

BEFFA, L. M., VAN WYK, J. B., and G. J. ERASMUS. 2009a. Long-term selection experiment with Afrikaner cattle. 1. Environmental factors affecting calf growth. *South African Journal of Animal Science* 39:89-97.

BEFFA, L. M., VAN WYK, J. B., and G. J. ERASMUS. 2009b. Long-term selection experiment with Afrikaner cattle. 2. Genetic parameters and genotype by environment interaction for calf growth traits. *South African Journal of Animal Science* 39:98-105.

BEFFA, L. M., VAN WYK, J. B., and G. J. ERASMUS. 2009c. Long-term selection experiment with Afrikaner cattle. 3. Selection applied and selection response in calf growth traits. *South African Journal of Animal Science* 39:106-113.

BEFFA, L. M., VAN WYK, J. B., and G. J. ERASMUS. 2009d. Long-term selection experiment with Afrikaner cattle. 4. Cow fertility and calf survival. *South African Journal of Animal Science* 39:114-126.

BELLOWS, R. A., SHORT, R. E., ANDERSON, D. C., KNAPP, B. W., and O. F. PAHNISH. 1971. Cause and effect relationships associated with calving difficulty and calf birth weight. *Journal of Animal Science* 33:407-415.

BESTER, J., MATJUDA, L. E., RUST, J. M., and H. J. FOURIE. 2003. Nguni: a case study. In. Vilakati *et al*. (eds) 2003. Community-based management of animal genetic resources. Rome: FAO.

BOICHARD, D., MAIGNEL, L., and E. VERRIER. 1997. The value of using probabilities of gene origin to measure genetic variability in a population. *Genetics, Selection and Evolution* 29:5-23.

BOTHMA, A. J. 1993. Comparison of the government Nguni studs in Venda. MSc Thesis, University of Pretoria.

BOURDON, R. M. 1997. Understanding animal breeding. Prentice-Hall. New Jersey.

BOURDON, R. M. 1998. Shortcomings of current genetic evaluation systems. Journal of Animal Science 76: 2308-2323.

BOZZI, R., FRANCI, O., FORABOSCO, F., PUGLIESE, C., CROVETTI, A., and F. FILIPPINI. 2006. Genetic variability in three Italian beef cattle breeds derived from pedigree information. *Italian Journal of Animal Science* 5:129-137.

BRIGHT, G. 1991. Economic weights from profit equations: appraising their accuracy. *Animal Production* 53:395-398.

BRINKS, J. S., MCINERNEY, M. J., and P. J. CHENOWETH. 1978. Relationship of age at puberty in heifers to reproductive traits in young bulls. In: *Proceedings of the Western Section of the American Society of Animal Science* 29:28-30.

BRINKS, J. S., CLARK, R. T., and F. J. RICE. 1961. Estimation of genetic trend in beef cattle. *Journal of Animal Science* 20:903 (Abstract).

BULMER, M. G. 1985. The Mathematical Theory of Quantitative Genetics. Clarendon Press, Oxford, UK.

BURROW, H. M., SEIFERT, G. W., and D. J. S. HETZEL 1991. Consequences of in the selection for weaning weight in Zebu, Bos Taurus and Zebu x Bos Taurus Cattle in the Tropics. *Australian Journal of Agricultural Research* 42:295-307.

CLEVELAND, M. A., BLACKBURN, H. D., ENNS, R. M., and D. J. GARRICK. 2005. Changes in inbreeding of U.S. Herefords during the twentieth century. *Journal of Animal Science* 83:992-1001.

DALTON, D. C. 1980. An introduction to practical animal breeding. Granada Publishing, Great Britain.

DEKKERS, J. C. M., and J. P. GIBSON. 1998. Applying breeding objectives to dairy cattle improvement. *Journal of Dairy Science* 81:19-35.

DEPARTMENT OF AGRICULTURE – REPUBLIC OF SOUTH AFRICA. 2008. National agricultural research and development strategy.

http://www.info.gov.za/view/DownloadFileAction?id=122476

DICKERSON, G. E. 1969. Experimental approaches in utilizing breed resources. *Animal Breeding Abstracts* 37:191-202.

DICKERSON, G. E. 1970. Efficiency of animal production – molding the biological components. *Journal of Animal Science* 30:849-859.

DICKERSON, G. E., BLUNN, C. T., CHAPMAN, A. B., KOTTMAN, R. M., KRIDER, J. L., WARWICK, E. J., and J. A. WHATLEY, Jr. 1954. Evaluation of selection in developing inbred lines of swine. North Central Regional Pub. 38, Missouri Research Bulletin No. 551.

ENGLISH, P. R., FOWLER, V. R., BAXTER, S., and B. SMITH. 1996. The growing and finishing pig: Improving efficiency. Farming Press: London

FALCONER, D. S., and T. F. C. MACKAY. 1996. Introduction to Quantitative Genetics. 4th ed. Pearson Education Ltd. Harlow, U.K.

FERRELL, C. L., and T. G. JENKINS. 1984. Relationships among various body components of mature cows. *Journal of Animal Science* 58:222-233.

FOOD AND AGRICULTURE ORGANIZATION (FAO). 1998. Secondary guidelines for development of national genetic resource management plans. Pages 53-62.

GAMA, L. T., and N. CAROLINO. 2002. Demographic analysis of the Alentejana breed of cattle. 7th World Congress on Genetics Applied to Livestock Production, August 19-23, Montpellier, France.

GIBSON, J. P., and B. W. KENNEDY. 1990. The use of constrained selection indexes in breeding for economic merit. *Theoretical and Applied Genetics* 80:801-805.

GODDARD, M. E. 1998. Consensus and debate in the definition of breeding objectives. *Journal of Dairy Science* 81: 6-18.

GROEN, A. F. 2000. Breeding goal definition. In: S. Galal, J. Boyazoglu and K. Hammond. Proceedings of the workshop on developing breeding strategies for lower input animal production environments. *ICAR Technical Series* 3:25-104.

GUIDELINES FOR UNIFORM BEEF IMPROVEMENT PROGRAMS. 2010. 9th Edition. www.beefimprovement.org

HAMBURGER, H., and K. A. RAMSAY. 1984. The current status and future of animal production and breeding in developing countries: The Southern African region. *In*: J. H. Hofmeyr and E. H. H. Meyer (eds.) *Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding*. Pretoria.

HARRIS, D. L. 1970. Breeding for efficiency in Livestock Production: Defining the economic objectives. *Journal of Animal Science* 30:860-865.

HARRIS, D. L., and S. NEWMAN. 1994. Breeding for profit: Synergism between genetic improvement and livestock production. A review. *Journal of Animal Science* 72:2178-2200.

HAZEL, L. N. 1943. The genetic basis for construction selection indexes. *Genetics* 28: 476-490.

HAZEL, L. N., DICKERSON, G. E., and A. E. FREEMAN. 1994. Symposium: Selection index theory. The selection index – Then, now and for the future. *Journal of Dairy Science* 77:3236-3251.

HOFMEYR, J.H. 1994. Findings of a committee on a genebank for livestock. Proc. Conf. Conservation Early Domesticated Animals of Southern Africa, Pretoria, 3-4 March.

JAMES, J. W. 1982. Construction, uses and problems of multitrait selection indices. *Proceeding of the 2nd World Congress on Genetics Applied to Livestock Production*. Madrid.

JUGA, J., and R. THOMPSON. 1989. Estimation of variance components in populations selected over generations. *Acta Agriculturae Scandinavica* 39: 79-89.

KENNEDY, B. W. 1990. Mixed model methodology in analysis of designed experiments. Pages 76–94 in Advances in Statistical Methods for Genetic Improvement of Livestock. D. Gianola and K. Hammond, ed. Springer-Verlag, Berlin, Germany.

KLUYTS, J. F., NESSER, F. W. C., and M. J. BRADFIELD. 2003. Development of breeding objectives for beef cattle breeding: Derivation of economic values (Review article). *South African Journal of Animal Science* 33:142-158.

KOCH, R. M., GREGORY, K. E., and L. V. CUNDIFF. 1974. Selection in beef cattle. I. Selection applied and generation interval. *Journal of Animal Science* 39:449-458.

KOCH, R. M., CUNDIFF, L. V., and K. E. GREGORY. 1994. Cumulative Selection and genetic change for weaning or yearling weight or for yearling weight plus muscle score in Hereford cattle. *Journal of Animal Science* 72:864-885.

LANDE R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution* 34:292–305.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science* 241: 455-1460.

LESLIE, P. H. 1945. The use of matrices in certain population mathematics. *Biometrika* 33:183–212.

LESLIE, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213–245.

LUESAKUL REODECHA, C., MARTIN, T. G., and L. A. NELSON. 1986. Effects of long-term selection for 365-day weight on maternal performance of beef cows. Pages 205-209 in *Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production*. Lincoln, Nebraska.

LUSH, J. L. 1946. Chance as a cause of changes in gene frequency within pure breeds of livestock. American Naturalist 80:318-342.

LYNCH, M., and B. WALSH. 1998. Genetics and analysis of quantitative traits. Sinauer: Sunderland, Massachusetts.

MACKINNON, M. J., HETZEL, D. J. S., CORBET, J. J., BRYAN, R. P., and R. DIXON. 1990. Correlated responses to selection for cow fertility in a tropical beef herd. *Animal Production* 50:417-424.

MACNEIL, M. D., and L. E. MATJUDA. 2007. Breeding objectives for Angus and Charolais specialized sire lines for use in the emerging sector of South African beef production. *South African Journal of Animal Science* 37:1-10.

MACNEIL, M. D., URICK, J. J., and W. M. SNELLING. 1998. Comparison of selection by independent culling levels for below average birth weight and high yearling weight with mass selection for high yearling weight in line 1 Hereford cattle. *Journal of Animal Science* 76:458-467.

MACNEIL, M. D., CUNDIFF, L. V., DINKEL, C. A., and R. M. KOCH. 1984. Genetic correlations among sex-limited traits in beef cattle. *Journal of Animal Science* 58:1171-1179.

MACNEIL, M. D., NUGENT, R. A., and W. M. SNELLING. 1997. Breeding for profit: an introduction to selection index concepts. *Proceeding of the Range Beef Cow Symposium* XV. Rapid City, South Dakota.

MACNEIL, M. D., and S. NEWMAN. 1992. Relative economic values for traits affecting profitability of beef production in Canada. *Proceedings of the Beef Improvement Federation*. Portland, Oregon.

MACNEIL, M. D., and T. B. MOTT. 2000. Using genetic evaluations for growth and maternal gain from birth to weaning to predict energy requirements of Line 1 Hereford beef cows. *Journal of Animal Science* 78:2299-2304.

MAGEE, W. T. 1965. Estimating response to selection. *Journal of Animal Science* 24: 242-247.

MATJUDA, L. E. 2005. The role of the Angus breed in the emerging beef sector in South Africa. *Proceedings of the 9th World Angus Forum Technical Meeting*. Cape Town, 19 March, pg. 61-65.

MCPARLAND, S., KEARNEY, J. F., RATH, M., and D. P. BERRY. 2007. Inbreeding effects on milk production, calving performance, fertility, and conformation in Irish Holstein-Friesians. *Journal of Dairy Science* 90:4411-4419.

MELTON, B. E. 1995. Conception to consumption: The economics of genetic improvement. *Proceedings of the Beef Improvement Federation*. Sheridan, WY.

MERCADANTE, M. E. Z., PACKER, I. U., RAZOOK, A. G., CYRILLO, J. N. S. G., and L. A. FIGUEIREDO. 2003. Direct and correlated responses to selection for yearling–weight on reproductive performance of Nelore cows. *Journal of Animal Science* 81:376-384.

MEUWISSEN, T.H.E., and J. A. WOOLLIAMS. 1994. Effective sizes of livestock populations to prevent a decline in fitness. *Theoretical and Applied Genetics* 89:1019-1026.

MEYER, E. H. H. 1984. Chromosomal and biochemical genetic markers of cattle breeds in southern Africa. Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding, pg. 328-339.

MEYER, K., HAMMOND, K., MACKINNON, M. J., and P. F. PARNELL. 1991. Estimates of covariances between reproduction and growth in Australian beef cattle. *Journal of Animal Science* 69:3533-3543.

MORRIS, C. A., BAKER, R. L., and J. C. HUNTER. 1992. Correlated responses to selection for yearling or 18-month weight in Angus and Hereford cattle. *Livestock Production* 30:33-52.

MRODE, R. A. 1988. Selection experiments in beef cattle. Part 2: A review of responses and correlated responses. *Animal Breeding Abstracts* 56: 155-167.

MRODE, R. A., SMITH, C., and R. THOMPSON. 1990. Selection for rate and efficiency of lean gain in Hereford cattle. 2. Evaluation of correlated responses. *Animal Production* 51:35-46.

NATIONAL BEEF RECORDING AND IMPROVEMENT SCHEME. 2007. Livestock Business Division, Animal Improvement Institute of South Africa.

NDUMU, D. B., BAUMUNG, R., WURZINGER, M., DRUCKER, A. G., OKEYO, A. M., SEMAMBO, D., and J. SOLKNER. 2008. Performance and fitness traits versus phenotypic appearance in the African Ankole Longhorn cattle: A novel approach to identify selection criteria for indigenous breeds. *Livestock Science* 113:234-242.

NELSON L. A., and G. D. BEAVERS. 1982 Beef x beef and dairy x beef females mated to Angus and Charolais sires. I. Pregnancy rate, dystocia and birth weight. *Journal of Animal Science* 54:1138-1149.

NEWMAN, S., MORRIS, C. A., BAKER, R. L., and G. B. NICOLL. 1992. Genetic improvement of beef cattle in New Zealand: Breeding objectives. *Livestock Production Science* 32:111-130.

NEWMAN, S., MACNEIL, M. D., GOLDEN, B., and S. BARWICK. 1994. Implementation and use of selection indexes in genetic improvement schemes for beef cattle. *Proceedings of the 4th Genetic Prediction Workshop, Beef Improvement Federation*. Kansas City, Missouri.

NICHOLAS, F. W. 1989. Incorporation of new reproductive technology in genetic improvement programmes. *In:* W. G. Hill and T. F. C. MacKay (ed.) *Evolution and Animal Breeding*. CAB International, Wallingford, UK.

NOMURA, T., HONDA, T., and F. MUKAI. 2001. Inbreeding and effective population size of Japanese Black Cattle. *Journal of Animal Science* 79:366-370.

NOTTER, D. R., CUNDIFF, L. V., SMITH, G. M., LASTER, D. B., and K. E. GREGORY. 1978. Characterization of biological types of cattle. VI. Transmitted and maternal effects on birth and survival traits in progeny of young cows. *Journal of Animal Science* 46:892-907.

NÚÑEZ-DOMINGUEZ, R., CUNDIFF, L. V., DICKERSON, G. E., GREGORY, K. E., and R. M. KOCH. 1991. Lifetime production of beef heifers calving first at 2 vs 3 years of age. *Journal of Animal Science* 69:3467-3479.

NWAKALOR, L. N., BRINKS, J. S., and G. V. RICHARDSON. 1986. Selection in Hereford cattle. I. Selection intensity, generation interval and indexes in retrospect. *Journal of Animal Science* 62:927-936

OLESEN, I., GROEN, A. F., and B. GJERDE. 2000. Definition of animal breeding goals for sustainable production systems. *Journal of Animal Science* 78:570-582.

PASTERNAK, H. and J. I. WELLER. 1993. Optimum linear indices for non-linear profit functions. *Animal Production* 55:43-50.

PEARSON, R. E. 1982. Economic aspects of the choice of a breeding objective. *Proceedings of the 2nd World Congress on Genetics Applied to Livestock Production*. VI: 50-59.

PHOCAS, F., BLOCH, C., CHAPELLE, P., BECHEREL, F., RENAND, G., and F. MENSSIER. 1998. Developing a breeding objective for a French purebred beef cattle selection programme. *Livestock Production Science* 57:49-65.

PONZONI, R. W., and S. NEWMAN. 1989. Developing breeding objectives for Australian beef cattle breeding. *Animal Production* 49:35-47.

POTTER, L., LOBATO, J. F. P., and C. G. A. M. NETTO. 1998. Productivity of a model of production for primiparous beef heifers at two, three and four years of age. *Brazilian Journal of Animal Science* 27:613-619

QUAAS, R. L. 1976. Computing the diagonal elements and inverse of a large numerator relationship matrix. *Biometrics* 32:949-953.

PRESTON, T. R., and M. B. WILLIS, 1974. Intensive Beef Production (2nd edition). Pergamon Press, Oxford, UK.

REGE J. E. O. 2001. Defining livestock breeds in the context of community based management of farm Animal Genetic Resources. In Proc. Workshop on Community Based Management of Animal Genetic Resources. Mbabane, Swaziland. May 7 – 11. FAO corporate repository.

REGE, J. E. O. and C. L. TAWAH. 1999. The state of African cattle genetic resources: II. Geographical distribution, characteristics and uses of present-day breeds and strains. *Animal Genetic Resources Information*. 26:1-25.

ROBERTSON, A. 1959. The sampling variance of the genetic correlation coefficient. *Biometrics* 15:469-485.

ROCKWOOD, L. L. 2006. Introduction to population ecology. Blackwell Publishing. Oxford, UK.

ROFF, D. A. 1997. Evolutionary Quantitative Genetics. Chapman & Hall: New York.

ROGERS, P. L., GASKINS, C. T., JOHNSON, K. A., and M. D. MACNEIL. 2004. Evaluating longevity of composite beef females using survival analysis. *Journal of Animal Science* 82:860-866.

ROUGHSEDGE, T., AMER, P. R., THOMPSON, R. and G. SIMM. 2005. Development of a maternal breeding goal and tools to select for this goal in UK beef production. *Animal Science* 81:221-232.

SCHNEEBERGER, M., BARWICK, S. A., CROW, G. H. and K. HAMMOND. 1992. Economic indices using breeding values predicted by BLUP. *Journal of Animal Breeding and Genetics* 109:183-193.

SCHOLTZ, M. M., and K. A. RAMSAY. 2007. Experience in establishing a herd book for the local Nguni breed in South Africa. *Animal Genetic Resources Information* 41:25-28.

SCHOLTZ, M. M., and C. Z. ROUX. 1984. Correlated responses to selection for growth, size and efficiency. *Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding* 1:1-11.

SCHOLTZ, M. M. 1988. Selection possibilities of hardy beef breeds in Africa: the Nguni example. In: *Proceedings of the 3rd World Congress on Sheep and Beef Cattle Breeding*. Paris, France.

SCHONS, D., HOHENBOKEN, W. D., and J. D. HALL. 1985. Population analysis of a commercial beef cattle herd. *Journal of Animal Science* 61:44-54.

SIVARAJASINGAM, S. 1995. A method to estimate economic weights for traits if disease resistance in sheep. *Proceedings of the Australian Association for the Advancement of Animal Breeding and Genetics* 11:65-69.

SNELLING, W. M., GOLDEN, B. L., and R. M. BOURDON. 1995. Within herd genetic analyses of stayability of beef females. *Journal of Animal Science* 73:993-1001.

SORENSEN, A. C., SORENSEN, M. K., and P. BERG. 2005. Inbreeding in Danish dairy cattle breeds. *Journal of Dairy Science* 88:1865-1872.

SORENSEN, D. A., and B. W. KENNEDY. 1984. Estimation of genetic variances from unselected and selected populations. *Journal of Animal Science* 59:1213-1223.

SOUTH AFRICAN LIVESTOCK BREEDING. 2004. Picasso Headline Pty Ltd. Cape Town, South Africa.

STRYDOM, P. E., NAUDE, R. T., SMITH, M. F., KOTZE, A., SCHOLTZ, M. M., and J. B. VAN WYK. 2001. Relationships between production and product traits in subpopulations of Bonsmara and Nguni cattle. *South African Journal of Animal Science* 31:181-194.

TANOA, K., KAMUANGAB, M., FAMINOWC, M. D., and B. SWALLOW. 2003. Using conjoint analysis to estimate farmer's preferences for cattle traits in West Africa. *Ecological Economics* 45:393-407.

TESS, M. W., BENNETT, G. L., and G. E. DICKERSON. 1983a. Simulation of genetic changes in life-cycle efficiency of pork production. I. A bioeconomic model. *Journal of Animal Science* 56:336-353.

TESS, M. W., BENNETT, G. L., and G. E. DICKERSON. 1983b. Simulation of genetic changes in life-cycle efficiency of pork production. II. Effects of components on efficiency. *Journal of Animal Science* 56:354-368.

TESS, M. W., G. L. BENNETT AND G. E. DICKERSON. 1983c. Simulation of genetic changes in life-cycle efficiency of pork production. III. Effects of management systems and feed prices on importance of genetic components. *Journal of Animal Science* 56:369-379.

VAN ARENDONK, J. A. M. 1985. Studies on the replacement policies in dairy cattle. II. Optimum policy and influence of changes in production and prices. *Livestock Production Science* 13:101-121.

VAN DER WESTHUIZEN, J., and L. E. MATJUDA. 1999. Breeding objectives. In: Beef breeding in South Africa (Ch. 5). Ed. Scholtz., M.M., Bergh, L. and Bosman, D.J., Agricultural Research Council - Animal Improvement Institute, Irene, pp 27.

VAN VLECK, L. D. 1993. Selection Index and introduction to a mixed model methods. CRC Press. Boca Raton, Florida.

YAMADA, Y. 1977. Evaluation of the culling variate used by breeders in actual selection. Genetics 86: 885-899.

# APPENDIX

Computer program for simulation of life-cycle production starting with 1000 Nguni heifer calves; implemented using SAS (SAS Institute Inc., Cary North Carolina, USA).

```
data econ_val;

* The breed under consideration is the NGUNI;

seed = 75831;

v_hfr = 14.0;                         * value/kg of replacement heifer;

bwt = 26;                             * birth weight;

cv_ww = 0.12;                         * coefficient variation in weaning weight - verify using actual
                                        data;

mp = 825;                             * initial parameter for milk production;

g1 = 138;                             * initial parameter for weaning weight - average gain from birth to
                                        weaning;

ww_d = 0; ww_m = 0;                   * direct and maternal additive effects;

wwt = bwt + g1 + ww_d + ww_m;         * weaning weight of calves;

h_wwt = 0.95*wwt;                     * initial weight of heifers;

mp = mp + 20.5*ww_m;                  * assumes conversion milk:gain of 20.5:1;

m_wt = 364;                           * initial parameter for mature weight;

dg1 = 1.15; df1 = 28;  fc1 = 5.00;    * growth rate, days on feed, feed conversion during adaptation
                                        period (Phase 1);

dg2 = 1.45; df2 = 127;  fc2 = 5.50;   * growth rate, days on feed, feed conversion during Phase 2;


dm_feed_price = 0.93;                 * price of feed kg DM;

cDM_1 = dm_feed_price*1.0;            * cost DM 1st post-weaning period - Phase 1;
cDM_2 = dm_feed_price*0.87;           * cost DM 2nd post-weaning period - Phase 2;

cDMm_1 = dm_feed_price*0.48;          * cost DM heifer development wean to 13 months;
cDMm_2 = dm_feed_price*0.32;          * cost DM heifer development 13 months to 19 months;

cDMm_3 = dm_feed_price*0.31;          * cost DM cows 6 months immediately pre-calving;
```

```
cDMm_4 = dm_feed_price*0.35;            * cost DM cows 6 months immediately post-calving;

fcFD = 0.92;                            * fixed cost /hd/d of feeding;

* carcass characterisation;

dp = 0.55;                              * dressing %;
fd = 6;                                 * fat depth at harvest;

c_pvi=0.0; c_pve = 0.0; c_npv = 0.0;    * set accumulators for present values of income, expenses and
net present value;

* decomposition of variance-covariance matrix;
* ordered fat depth (mm) and carcass weight (kg);

a1 = 0.46; a2 = 4.2; a3 = 12.3;

* carcass pricing information;
c_base = 20.0;
cw_lo = 185; cwp_wlo = -2.1;
cw_hi = 245; cwp_whi = -1.6;

flo = 1;   cwp_flo = -0.6;
fhi = 5;  cwp_fhi = -0.7;
fvh = 10; cwp_fvh = -1.2;

* diets and costs (R/kg) of feed energy for heifers and cows;

NEm_1 = 0.72;                           * net energy value of diet for maintenance fed to weaned heifer
                                          calf (age = 7 mo) raised as a replacement;

NEm_2 = 0.68;                            * net energy value of diet for maintenance fet to yearling (age =
                                           19 mo) replacement heifer;

NEm_3 = 0.50;                            * average net energy value of diet for maintenance of beef cow
                                           during 6 mo immediately pre-calving;

NEm_4 = 0.55;                            * average net energy value of diet for maintenance of beef cow
                                           during 6 mo immediately post-valving;

rate = 0.05;                             * applicable interest rate;

income = 0;                              * initialise income;

* raising replacement heifers;

yr = 1;

cow_wt = 0.67*m_wt;                      * weight of cull open heifer;
N = 1000;                                * initial number of heifers;

cull_cow_price = 13;

pg1 = 0.70; ccp = cull_cow_price;
n_females = N;
```

```
SBW1 = h_wwt;                          * initial shrunk body weight (kg);
SBW2 = cow_wt;                         * final shrunk body weight (kg);

MWT1 = ((SBW1 + SBW2)/2 + SBW1)/2;    * mid-weight 1st 6 mo;
MWT2 = ((SBW1 + SBW2)/2 + SBW2)/2;    * mid-weight 2nd 6 mo;

* calculation of dry matter intake using NRC equations;

DMI_1 = (MWT1**0.75*(0.2435*NEm_1 - 0.0466*NEm_1**2 - 0.1128))/NEm_1;
DMI_2 = (MWT2**0.75*(0.2435*NEm_2 - 0.0466*NEm_2**2 - 0.1128))/NEm_2;

* extrapolation to annual basis;

FC = (cDMm_1*DMI_1 + cDMm_2*DMI_2)*182.5;

* initial investment in heifer calves;

in_cost = h_wwt*v_hfr;

* discouned feed and non-feed cost of heifers for 1st year incurred daily over yr;

dsc = (1400 + FC)*exp(-rate);
pve1 = N*(in_cost + dsc);

* establish number of pregnant heifers and conversely number of open heifers to be sold;

do females = 1 to N;
  * pg_status = 0 denotes pregnant - pg_status = 1 denotes open;
  pg_status = ranuni(seed);
  seed = seed + 13;
  if pg_status <= pg1 then pg_status = 0;
  else do;
       pg_status = 1;
       n_females = n_females - 1;
     end;
  * income from sale of open heifers received at end of yr;
     income = income + pg_status*ccp*cow_wt;
end;

pvi1 = income*(1 + rate)**-yr;
npv1 = pvi1 - pve1;
feed_cost = N*dsc;

******************* 2nd year ******************************************;

do yr = 2 to 10;
  pvi = 0; pve = 0; npv = 0;
  cci = 0;                             * cull cow income accrues at preg. check;
  pvfc = 0;                            * present value of expense from current production cycle;
  sum_feed_cost = 0.;
  N = n_females;
  n_sv = 0;

  * set time dependent state variables;

  if yr = 2 then do;
```

```
   ivm = 0.01; pgr = 0.94; csv = 0.85; fmt = 0.87; ccp = cull_cow_price*1.00; aod = 0.85; end;
if yr = 3 then do;
   ivm = 0.03; pgr = 0.81; csv = 0.90; fmt = 0.92; ccp = cull_cow_price*0.97; aod = 0.90; end;
if yr = 4 then do;
   ivm = 0.02; pgr = 0.77; csv = 0.90; fmt = 0.98; ccp = cull_cow_price*0.94; aod = 0.95; end;
if yr = 5 then do;
   ivm = 0.03; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;
if yr = 6 then do;
   ivm = 0.04; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;
if yr = 7 then do;
   ivm = 0.05; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;
if yr = 8 then do;
   ivm = 0.06; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;
if yr = 9 then do;
   ivm = 0.08; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;
if yr = 10 then do;
   ivm = 0.10; pgr = 0.89; csv = 0.90; fmt = 1.00; ccp = cull_cow_price*0.94; aod = 1.00; end;


do females = 1 to N;
   sv_status = ranuni(seed);
   if sv_status <= csv then n_sv = n_sv + 1;

   pg_status = ranuni(seed);
   if pg_status > pgr then do;
                              n_females = n_females - 1;
                              cci = cci + ccp*fmt*m_wt;
                          end;
end;



* performance to weaning;

sd_ww = cv_ww*aod*wwt;
put n_sv yr;
do calves = 1 to n_sv;
if (yr = 2) and (calves <= (round(n_sv*0.01285*(bwt-26),1.))) then goto end1;

   dev = rannor(seed);
   calf_wt = aod*wwt + sd_ww*dev;

* end calcualting distribution of weaning weights;

* calculation of post-weaning performance;

* random numbers used in distribution of carcass traits;

   r1 = rannor(seed);
   r2 = rannor(seed);

* feeding system characterised by 28-d initial phase
  then a finishing phase for f_days;

  w1 = calf_wt + df1*dg1;
  dmi = dg1*fc1*df1;
```

```
    cDM_calf = dmi*cDM_1;

  * end of initial post-weaning period, begin second period;

    w2 = w1 + df2*dg2;
    dmi = dg2*fc2*df2;
    cDM_calf = cDM_calf + dmi*cDM_2;
    tof = df1 + df2;

  * carcass characteristics;

    cwt = dp*w2 + a2*r1 + a3*r2;
    dom = 100*(cwt/dp)/m_wt;
    con = 100*(220/dp)/m_wt;
    fat = fd + 0.037*(dom - con) + a1*r1;



  * income and expense;

    padj = 0.0;
    padg = 0.0;

    if cwt < cw_lo then padj = cwp_wlo;
    if cwt > cw_hi then padj = cwp_whi;
    if fat < flo then padg = cwp_flo;
    if fat >= fhi and fat < fvh then padg = cwp_fhi;
    if fat >= fvh then padg = cwp_fvh;
            d_price = padj + padg;
    price = c_base + d_price;

  * income from and expense for sale of calf;

    slage = 200 + tof;
    pv = price*cwt*(1+rate)**(-slage/365.25);
    pvi = pvi + pv;
    dsc = exp(-rate*tof/365.25);
    dfc = dsc*(cDM_calf + fcFD*tof);
    pvfc = pvfc + dfc*(1-rate)**-yr;

end1:   end; *of progeny finishing phase;

* calculation of dry matter intake for cows following NRC 1996;

SBW1 = 0.4355*cow_wt;                       * initial shrunk body weight (kg);
cow_wt = m_wt*fmt;                          * after Gregory et al., (1992);
SBW2 = 0.4355*cow_wt;                       * final shrunk body weight (kg);

MWT1 = ((SBW1 + SBW2)/2 + SBW1)/2;          * mid-weight 2nd & 3rd trimester;
MWT2 = ((SBW1 + SBW2)/2 + SBW2)/2;          * mid-weight 2-yr-old lactation;

* maintenance bit;

DMI_1 = (MWT1**0.75*(0.04997*NEm_3**2 + 0.04361))/NEm_3;
DMI_2 = (MWT2**0.75*(0.04997*NEm_4**2 + 0.0384))/NEm_4;
```

```
* lactation bit;                          * 0.3 kg TDN / kg milk; * 0.6 kg TDN / kg DM;

DMI_L = 0.5*MP/200;                               * prediction assuming 200 d lactation;
DMI_2 = DMI_2 + DMI_L;

* update number of females for involuntary culling;

n_cull = int(ivm*n_females);
n_females = n_females - n_cull;
cci = cci + n_cull*ccp*fmt*m_wt;

* extrapolation to annual basis and present value calculation, in $;

FC = (cDMm_3*DMI_1 + cDMm_4*DMI_2)*182.5;
pvcc = N*(FC + 1400.)*(1 + rate)**-yr;            * 1400 is estimate of fixed cost/cow;

* present value of income;

pv_cci = cci*(1 + rate)**-yr;
pvi = pvi + pv_cci;

*present value of expense;

pve = pvcc + pvfc;

* net present value;

npv = pvi - pve;

c_pvi = c_pvi + pvi;
c_pve = c_pve + pve;
c_npv = c_npv + npv;

put yr n_females c_pvi c_pve pvcc c_npv;

end; * of year loop;

* recover salvage value of remaining females;

pvs = n_females*m_wt*(1 + rate)**-10;
c_pvi = c_pvi + pvi1 + pvs;
c_pve = c_pve + pve1;
c_npv = c_pvi - c_pve;

sust = round((c_pvi/c_pve),.0001);
c_pvi = round(c_pvi/1000, .1);
c_pve = round(c_pve/1000, .1);
c_npv = round(c_npv/1000, .1);

keep c_pvi c_pve c_npv sust;


run;

proc print;
run;
```