Selection for beef traits and calving performance in Piemontese cattle

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Doctoral thesis

Abstract

Beef cattle selection programmes are usually focused on the improvement of production traits. However, also functional traits play an important role for the efficiency of animal production. Among these traits calving performance, affecting stillbirth of calves, fertility of cows, animal welfare and consumers' perception of products is particularly relevant for specialized beef cattle breeds. The aim of this thesis was the development of a programme for the improvement of calving performance and beef traits through selection in the Italian Piemontese cattle population. The breeding goal has been defined using both economic and biological approaches. The effect of production circumstances on the estimated economic and biological values has been discussed. Genetic parameters for calving performance have been estimated using animal models including direct and maternal additive genetic effects. Estimated heritabilities ranged from 0.05 for maternal effect in cows to 0.19 for direct effect in heifers. Direct and maternal effects showed strong negative genetic correlations. Estimated genetic relationships between calving performance and beef production traits were generally unfavourable, requiring the development of a specific selection strategy. Alternative breeding programmes have been implemented and compared in term of response to selection. Genetic improvement of beef traits and direct calving performance was obtained while maintaining the current genetic level of the population for maternal calving performance. The improvement of phenotypic expression of calving performance could only be achieved by including direct and maternal effects both in the breeding goal and in the index. Strategies allowing a reduction of generation interval proved to be crucial to allow genetic gain for beef traits. The selection of specialized paternal and maternal lines to be crossed increased the overall economic response of 20%. This scheme was the recommended strategy to select beef traits and calving performance, when allowed by the social structure of farms.

Contents

Chapter 1

General introduction

Introduction

Application of quantitative genetics theory to animal breeding and selection for production traits resulted in a dramatic increase in the efficiency and quality of animal production in the last 25 yr. In the last 10 yr, the importance of traits for the efficiency of animal production other than increased production has been recognised. These traits, mainly related to health and reproduction, are called functional traits. They affect the efficiency of production by reducing the costs of input as opposed to production traits that increase the amount of output (Groen et al., 1997). They also contribute to sustainability of production (Olesen et al., 2000), animal welfare and consumer's acceptability of products (Groen et al., 1997).

Multiple trait selection requires the definition of a breeding goal including individual traits weighted according to their relative contribution to efficiency of production as expressed by economic values (Hazel, 1943). Selection of animals to be parents of the next generation is based on a selection index weighting predictions of individual genetic merit for breeding goal traits by the economic values. Currently, the weight of functional traits in the selection index adopted in national programmes for dairy cattle ranges from 35 to 50% (Miglior et al., 2005).

In beef cattle, selection is mainly for traits related to beef production such as growth rate, conformation, dressing percentage and carcass composition. Little attention has been paid to functional traits in beef cattle breeding schemes. Among the functional traits, calving performance is important particularly for specialised beef breeds. These specialised beef breeds are characterized by large size or strong muscularity, showing relatively high incidence of calving problems. The ability to normally reproduce is important from an economic and animal welfare point of view, as well as for the future perspectives of a beef breed which also depend on its adaptability to a wide range of environmental conditions.

Economic importance of calving performance

Calving performance affects farm profit by the increase in the costs resulting from dystocia. Costs associated with dystocia in dairy cattle have been estimated by Meijering (1986); they include direct costs due to loss of the calf, veterinarian intervention, farmer labour and indirect costs due to reduced fertility and productivity of dams, resulting in increased culling rate. Veterinary fees and costs from unvoluntary culling of dams after a case of dystocia proved to be the highest components whereas the relevance of costs associated with stillbirth depended on the value of the calf.

Economic values for calving performance in dairy cattle have been estimated by Meijering (1986), Bekman and Van Arendonk (1993) and Dekkers (1994). Due to the categorical nature of the trait, economic values of calving performance are sensitive to the population level for calving difficulty.

In beef cattle, definition of breeding objectives has received little attention. Literature considered either the suckler cow or the fattening production systems separately (Amer et al., 1997; Hirooka et al., 1998). This led to the definition of different set of traits of interest according to the production system modelled. The contribution of functional traits to the economic efficiency of beef cattle production systems has been rarely investigated. Forabosco et al. (2005) computed economic values for reproduction traits and length of productive life in Chianina cattle. Very few studies estimated economic values also for calving performance. Due to the relatively high incidence of calving difficulties, the economic importance of this trait is larger in beef cattle than in dairy cattle. Koots and Gibson (1998), simulating an integrated production system, derived economic values for a number of traits, including calving performance. They found that all traits related to calf survival made significant contribution to the overall economic efficiency. Estimated economic values showed moderate dependence on the price of beef.

Genetic aspects of calving performance

Calving performance is usually recorded in the frame of national recording schemes. A system to classify calving performance according to the level of difficulty has been recommended (Philipsson et al., 1979) and is generally adopted. Five classes, ranging from spontaneous calving to embryotomy, are used by the farmers to subjectively score the calvings of the cows in their herd. National and international genetic evaluation procedures for calving performance have been routinely implemented in dairy cattle (Pasman et al., 2003).

Calving problems arise largely as a consequence of incompatibility between the size of the calf and the pelvic area of the dam (Philipsson et al., 1979). Therefore two biological components must be considered in the genetic analysis of calving performance: the calf effect and the dam effect (Meijering, 1986). As a consequence, the genetic model for analysing calving performance data includes a calf effect, identified as direct effect, reflecting the effect of the genotype of the calf, and a dam effect, identified as maternal effect, reflecting the effect of the genotype of the dam of the calf.

Several studies estimated genetic parameters for direct and maternal effects of calving performance in beef cattle providing the evidence of moderate but significant genetic variation for these traits (Trus and Wilton, 1988; Cubas et al., 1991; Varona et al., 1999). No estimates are available for double muscled breeds which show high levels of calving difficulties.

Calving performance in different parities is often considered as the expression of the same trait (Kemp et al., 1988; Cubas et al., 1991). However, the incidence of dystocia is usually much higher in the first compared to later parities, reflecting the relative immaturity of heifers at the moment of calving. Estimated genetic variances have been found to be heterogeneous across parities in dairy cattle (Cue, 1990), suggesting that calving performance in first and later parities should be considered as different traits.

Antagonistic genetic relationships between direct and maternal effects of calving performance are generally reported in literature (Burfening et al., 1981; Trus and Wilton, 1988) which can complicate the selection process. Selection effort to reduce calving problems acting on the calf size is counteracted by the negative effect that this exerts on the maternal component. For the design of optimum breeding programmes that include calving performance, the genetic correlations with production traits need to be considered,

particularly in beef cattle where conflicting relationships can be expected. However, the research area concerning genetic relationships between calving performance and traits related to beef production is almost unexplored. Few estimates of genetic correlations have been published with inconsistent results due to heterogeneous definition of the investigated beef traits and to the use of different estimation methods (Renand, 1985; Averdunk et al., 1987).

Selection strategies for calving performance have been studied in dairy cattle only, either ignoring (Philipsson et al., 1979) or setting to zero the genetic correlation with production traits (Meijering, 1986; Dekkers, 1994). Directional mating of bulls with best predicted breeding values for direct calving performance to heifers provides a good short-term solution to restrict dystocia problems, but does not lead to genetic improvement over time (Philipsson et al., 1979). Selection using a total merit index, including also direct and maternal effects of calving performance, produces a very little genetic improvement of calving traits with limited effect on milk production traits (Dekkers, 1994). However this strategy has been suggested to avoid independent culling of bulls for direct calving performance by the farmers (Dekkers, 1994). Little improvement is to be expected in dairy cattle when the economic benefit of reducing dystocia is counteracted by a reduction in the price of the newborn calf, due to lighter birth weight (Meijering, 1986). In beef cattle the situation is more complicated because production traits are likely to be correlated with calving performance and the weaned calf is the main revenue for the producers. There has been little research addressing these topics and, consequently, the knowledge on appropriate selection strategies for beef cattle is limited.

The Piemontese breed

The Piemontese breed is numerically the most important Italian beef breed, with a population of 135,000 cows (Direzione Sanità Pubblica.- Regione Piemonte, 2003). Piemontese cattle are highly specialized for beef production due to double muscling inducted by a specific mutation of myostatin gene (*mh*) located on Chromosome 2 (Grobet et al., 1998). A recent research (Anaborapi, 2004) estimated a frequency of 0.98 for the mutated allele in the Piemontese female populations, whereas all AI bulls were homozygous

for the same allele. Double muscling exerts positive effects on dressing percentage, carcass conformation and meat quality, but its influence on maternal traits such as calving performance is generally negative (Ménissier, 1982).

The breeding goal of the Piemontese breed includes traits related to quantitative beef production. Growth rates and muscularity of animals have been consistently improved through selection (Anaborapi, 2004). These traits are selected by performance testing on station of young bulls based on own performance for average daily gain and muscularity, appraised by classifiers through morphological evaluation. Station testing of bulls allows for shorter generation interval and higher selection intensity compared to progeny testing scheme. Accuracy of genetic prediction, even if based on single phenotypic information, is acceptable due to high values of estimated heritabilities for traits measured during performance testing, resulting from the reduction of environmental variance.

Since 1989 a recording system of calving performance according to the level of difficulty, based on the International Committee for Animal Recordings recommendations, has been adopted. Calving records are recorded by technicians visiting the controlled farms monthly. Initially farmers were provided with information about bulls based on simple phenotypic means of progeny corrected for herd effect. This allowed to roughly identifying bulls with easy born progeny or easy calving daughters. Since 2000 an animal model genetic evaluation procedure for direct and maternal calving performance has been introduced, as a consequence of the research conducted within this thesis. Starting from the same year, calving performance was included in the breeding goal using empirical weights.

Aim and outline of this thesis

This thesis aims to explore opportunities to improve calving performance and beef traits in the Italian Piemontese population through genetic selection. This requires knowledge on the breeding goal and genetic parameters for all traits in order to implement a genetic evaluation routine and establish a selection index.

Chapter 2 deals with the definition of the breeding goal including calving performance and beef production traits. A bio-economic model is developed to study the contribution of individual traits to the efficiency of an integrated beef production system. The model is used to estimate economic and biological values of the considered traits. The effects exerted by

production circumstances on the formulated breeding objective are also studied through sensitivity analysis.

Chapter 3 focuses on the estimation of genetic parameters for calving performance using linear animal models including correlated direct and maternal genetic effects. Calving records in the first and later parities are analysed separately to estimate direct and maternal heritabilities and direct-maternal genetic correlations across parities. A joint analysis with a multiple traits model is conducted to estimate genetic (co)variances between calving performance in different parities. The later analysis enables an appraisal of the predictive value of information collected on adult cows for the genetic merit of calving performance in heifers.

In Chapter 4 genetic parameters are estimated for beef production traits, growth and muscularity, measured during the performance test of young bulls. Estimates of genetic parameters for growth traits are widely available in literature. However, the performance testing procedure of Piemontese bulls has some specificities such as the very young age of calves at the beginning of the test or the length of the testing period that are uncommon for beef cattle. These characteristics, reducing the effect of pre-test environmental conditions, affect the magnitude of estimated genetic parameters.

Chapter 5 deals with the estimation of genetic (co)variances and correlations between calving performance and beef production traits. Genetic analyses are performed using multiple traits models which combine beef traits measured on station with calving scores collected in the farms. Calving scores include offspring birth records and daughters calving records of bulls station tested for beef traits. The estimates are used in the last chapter for the evaluation of alternative selection strategies and the construction of the selection index.

In the General Discussion, the development of a selection strategy is addressed. Firstly, cumulative discounted expressions for the traits included in the breeding goal are calculated. They account for the unequal contribution of selected animals, both in rate and timing, to the future generations in the different traits. Then, a selection index is set up using the estimated genetic parameters and discounted economic values. Alternative indices are derived using desired gains approach and the use of objective versus non-objective methods in deriving selection index is discussed for this specific situation. Response to selection is calculated using deterministic simulation. Sequential selection is simulated: bulls are first selected for beef traits after performance testing on station and then selected bulls are progeny tested for calving performance. Alternative breeding schemes are compared, differing for the proportion of animals selected in the different stages, the accuracy of the predicted breeding

values, the length of the progeny testing. Breeding programmes including the use of different sire and dam lines, selected according different breeding objectives, are also considered. Issues concerning the use of single or multiple lines programmes are discussed. Finally, topics related to the development and perspectives for the Piemontese breed are addressed.

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Chapter 2

Definition of a breeding goal for the Piemontese breed: economic and biological values and their sensitivity to production circumstances

A. Albera, P. Carnier, and A. F. Groen

Abstract

Economic values have been derived for the Piemontese breed using a bio-economic deterministic model that simulates an integrated beef cattle enterprise. Investigated traits were post-weaning daily gain (DG), live fleshiness scores (FLESH) that are related to the market value of animals for slaughter, calving ease in the first (CE_h) and later parities (CE_c) and calving interval (CI). Economic values, calculated using a fixed number of cows per herd as a basis of evaluation and expressed in Euro per cow per year, were 0.20 per g/d for DG, 57.01 per point for FLESH (measured with a linear scoring system in 9 classes), -2.60 per day for CI. For calving ease economic values per a 1% increase in the liability scale were 0.57 € in the first and 1.99 € in later parities respectively.

The economic value of the studied traits showed moderate dependence on trait levels. Production circumstances poorly affected the estimated economic values with the exception of energy input and live weight output limitations, that markedly decreased the economic values of all traits but FLESH. Biological values, reflecting improvement in efficiency in energy utilization, corresponded well in relative size to economic values in most of the considered traits.

Keywords: Breeding goals, Economic values, Biological values, Beef cattle

Introduction

The general aim of genetic improvement of farm animals is the increase in efficiency of production. Harris et al. (1984) and Ponzoni and Newman (1989) stressed the importance of a formal definition of the breeding goal as a relevant step in the development of breeding programmes. Choice of traits to be included in the breeding goal should be based on the relative contribution of each trait to the overall efficiency of production, usually evaluated from an economic perspective (Goddard, 1998). The breeding goal is formally defined by setting up an aggregate genotype to be improved, that is a function of individual genetic merit weighted by economic values of traits, i.e. their relative economic importance (Hazel, 1943). Bio-economic models, describing biological and economic aspects of livestock production systems, have been used extensively to derive economic values in beef cattle (Hirooka et al., 1998), dairy cattle (Groen, 1989a,b) and poultry (Jiang et al., 1998).

Beef cattle production is segmented into two different levels, involving the suckler cows and the fattening production system. Such a fragmentation has often led to a level specific breeding objective (Simm et al., 1986; Amer et al., 1996; Wilton and Goddard, 1996), albeit superior genetics will be expressed in different segments (Koots and Gibson, 1998a). Jiang et al. (1998) following the theory by Brascamp et al. (1985) illustrated that the economic values for the integrated or non-integrated production systems differ when there is a differentiation between cost price and market price of the products transferred from one segment to the next. Because this situation might hold also for beef cattle (e.g. for the price of the weaned calves), the model should appropriately reflect the production system for which breeding goals are defined.

Groen (1989c) investigated the influence of production circumstances on estimated economic values. Production circumstances include management system, market system and performance data and affect economic values mainly through changes in the price of products and cost of production factors or in the production levels. Also, limitations on outputs or inputs of the production system can exert important effects on the derivation of economic values (Gibson, 1989; Groen, 1989b). Only few studies investigated the sensitivity of estimated economic values to production circumstances in beef cattle (Hirooka et al., 1998; Koots and Gibson, 1998b).

In the breeding programme of the Italian Piemontese breed a selection criterion has been established based on predicted breeding values for beef traits (Albera et al., 2001) and

calving ease (Carnier et al., 2000). However a formal definition of the breeding goal and an economic selection index are still lacking for this breed.

The objective of the present study is to derive economic and biological values for traits affecting the efficiency of a Piemontese cattle farm. A sensitivity analysis is conducted in order to assess the robustness of estimated values to production circumstances, including the influence exerted by limitations on inputs and outputs of the system.

Material and Methods

General aspects of the model

In this study a bio-economic simulation model is developed to describe an integrated beef cattle enterprise. The model is deterministic and simulates inputs and outputs of a farm per year including breeding of suckler cows and fattening up to slaughter weight of all male calves and female calves not needed as replacements.

The model allows to compute economic values for a number of traits related to production and functionality of animals and can also be used to evaluate the biological efficiency of production, i.e. the efficiency of energy utilization for production, and to compute biological values of traits.

A schematic representation of the elements of the model is in Figure 1.

The number of suckler cows per herd is fixed at 50 units. The number of cows is rescaled only when applying limitations to the input of production factors or output of products. The calving season is equally distributed over the whole year. Weaning of calves takes place at an age of 6 months. After weaning, breeding females are reared and inseminated before 18 months of age and all pregnant females calve for the first time within 28 months of age. A 100% rate of artificial insemination is assumed. Weaned male and female calves not used for replacement are fattened and slaughtered at a fixed weight, 580 and 450 kg respectively. In the model purchase of animals is not considered, which means that fattening is restricted to the animals born at the farm. Culled cows are sold for slaughter after a finishing period.
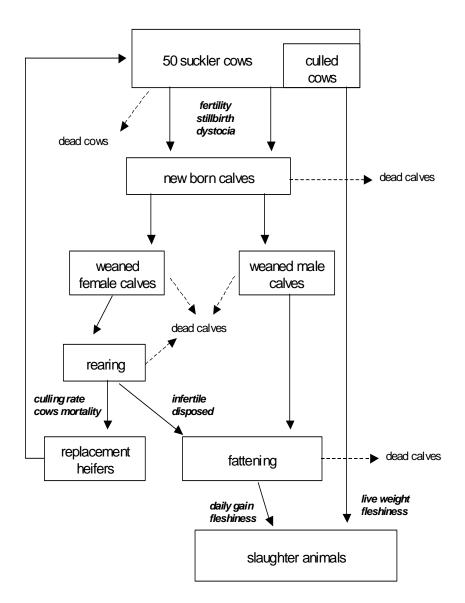
```
┌──────────────────────────────────────┐
│  50 suckler cows        ┌──────────┐  │
│                         │  culled  │  │
│                         │  cows    │  │
└─────────────────────────┴──────────┘
```

fertility
stillbirth
dystocia

dead cows

new born calves → → → dead calves

weaned female calves   weaned male calves

dead calves

rearing

culling rate *cows mortality*   *infertile* *disposed*

replacement heifers   fattening → → → dead calves

daily gain *fleshiness*   *live weight* *fleshiness*

slaughter animals

Figure 1. General representation of the elements of the model

Table 1. Animal, management and economic parameters used in the base situation.

Parameter	Value
Slaughter weight of young bulls (kg)	580
Slaughter weight of heifers (kg)	450
Mature weight of cows (kg)	637
Age at weaning (d)	180
Pre-weaning gain males (kg*d^{-1})	0.86
Pre-weaning gain females (kg*d^{-1})	0.80
Post-weaning gain males (kg*d^{-1})	1.25
Post-weaning gain females (kg*d^{-1})	1.0
Calving interval (d)	392
Culling rate of cows (%)	20.9
Mortality up to weaning (%)	1
Mortality during fattening (%)	2
Mortality of cows (%)	1
Slaughter price of young bulls (€*kg live weight^{-1})	3.10
Slaughter price of heifers (€*kg live weight^{-1})	3.51
Price of energy for fattening (€*MJ Net Energy^{-1})	0.022
Price of energy for cows (€*MJ Net Energy^{-1})	0.019
Cost of farmer labour (€*hour^{-1})	5.16
Cost of cesarean section (€)	113.62
Fixed costs for the farm (€*year^{-1})	21,309
Fixed costs per cow (€*year^{-1})	313
Fixed costs per fattened animal (€*year^{-1})	162

Revenues of the farm originate from the sale of slaughter animals (young bulls, heifers and culled cows), manure and from governmental subsidies. Costs are related to feeding of animals, labour, housing, machinery, health and insemination, and interest on investments.

The model calculates economic parameters, such as herd profit, profit per cow or cost price per kg of live weight of slaughter animals. The evaluation of biological efficiency of the production system is performed using net energy consumption per cow or per unit of product.

Traits considered in the model are post-weaning daily gain of fattened animals (DG), live fleshiness scores (FLESH), calving ease for heifers (CE_h) and cows (CE_c) and calving interval (CI). The model allows non-integer numbers of animals and assumes absence of genetic variation among animals.

Performance data and economic parameters used in the model and assumed as representative for the base situation are summarized in Table 1.

Herd composition

For suckler cows two age classes are considered: first and later parities. Composition of these classes is derived using fixed culling rates (data from the Piemontese Herdbook; Albera, unpublished). Number of male (N_{mw}) and female (N_{fw}) calves weaned per year is:

$$N_{mw} + N_{fw} = 0.5 \times [N_{c1} \times (2 - Still_{m1} - Still_{f1}) + N_{c2} \times Fert \times (2 - Still_{m2} - Still_{f2})] \times$$
$$\times (1 - Mort_w) \tag{1}$$

where N_{c1} and N_{c2} is the number of cows in age class 1 and 2, *Fert* is the proportion of later parity cows giving birth per year, *Still* are the stillbirth rates of calves within age class of dams and sex, and $Mort_w$ is the mortality rate up to weaning (fixed). Both *Fert* and *Still* are assumed to be affected by the level of dystocia, evaluated through calving performance scores (Carnier et al., 2000). Their values result from the weighted mean of calving scores incidence and relative fertility (level of dystocia in comparison with an easy calving causes a 2 to 12% increase of the calving interval, Albera, unpublished data) or stillbirth level (Albera et al., 1999). Three different age classes are defined for breeding heifers after weaning: from 6 to 12 months, from 13 to 18 months and from 19 to 28 months when calvings occur. Number of weaned females needed for replacement per year (N_r) depends on the culling rate of cows and the replacement rate of heifers during the rearing period and is given by:

$$N_r = N_{c1} / (1 - Rr)^3 \tag{2}$$

where *Rr* is the replacement rate during the rearing period (from weaning to first

calving) in each heifers age class as a consequence of death ($Mort_r$) and disposal ($Disp$) due to poor performance and non-pregnancy (Wilton et al., 1974). The replacement rate *Rr* is assumed to be fixed across breeding heifers age classes. Therefore, the number of breeding heifers in age class i is:

$$N_{f_i} = N_r \times (1 - Rr)^i \tag{3}$$

Slaughter animals produced at the farm are young bulls, heifers and culled cows. The number of fattened young bulls is:

$$N_{ms} = N_{mw} \times (1 - Mort_f) \tag{4}$$

where $Mort_f$ is the mortality rate during the fattening period.

Females culled during the rearing period before being pregnant are fattened together with females not used for replacements. Then, the number of heifers for slaughter (N_{fs}) is:

$$N_{fs} = (N_{fw} - N_r) \times (1 - Mort_f) + N_{fc12} \tag{5}$$

where N_{fc12} is the number of heifers culled in age classes 1 and 2, computed as:

$$N_{fc12} = N_r \times Disp + N_r \times (1 - R_r) \times Disp \tag{6}$$

Heifers culled in age class 3 (N_{fc3}) and culled cows in age classes 1 and 2 (N_{cc1} and N_{cc2}) are also sold for slaughter after a finishing period. Their number is given by:

$$N_{fc3} = N_r \times (1 - R_r)^2 \times Disp \tag{7}$$

and

$$N_{cc1} + N_{cc2} = N_{c1} \times Cull_{c1} + N_{c2} \times Cull_{c2} \tag{8}$$

where $Cull_{c1}$ and $Cull_{c2}$ are the culling rates of first and later parities cows respectively.

Profit equations

Profit (P) of the farm per year is modelled as:

$$P = R_F + R_C + R_O - C_F - C_C - C_{FX} \tag{9}$$

where R_F are revenues from the sale of fattened young bulls and heifers, R_C are revenues from culled cows, R_O are other revenues, C_F are costs for fattening of young bulls and heifers, C_C are costs for suckler cows, breeding heifers and calves before weaning and C_{FX} are fixed costs for the farm.

Annual revenues from the fattening of young animals are:

$$R_F = N_{ms} \times Weight_{ms} \times Price_{ms} + N_{fs} \times Weight_{fs} \times Price_{fs} \tag{10}$$

where m and f subscripts refer to male and female animals respectively. Revenues depend on the number of animals fattened (N), their weight and value per kg of live weight (*Weight* and *Price*).

Revenues from culled cows are:

$$R_C = N_{fc3} \times Weight_{fc3} \times Price_{fc3} + N_{cc1} \times Weight_{cc1} \times Price_{cc1} + N_{cc2} \times Weight_{cc2} \times$$

$$\times Price_{cc2} \tag{11}$$

where $Weight_{fc3}$, $Weight_{cc1}$ and $Weight_{cc2}$ are weights of heifers culled in age class 3, cows culled in age class 1 and 2 respectively and $Price_{fc3}$, $Price_{cc1}$ and $Price_{cc2}$ are the corresponding prices per kg of live weight.

Other revenues (R_O) include EC subsidies for suckler cows and slaughter animals and incomes from the selling of manure.

Costs for the fattening of young animals are:

$$C_F = Feed_{ms} + Feed_{fs} + Fxd_{ms} \times LF_{ms} + Fxd_{fs} \times LF_{fs} + Fx_F \qquad (12)$$

where $Feed_{ms}$ and $Feed_{fs}$ are feeding costs for male and female animals, Fxd_{ms} and Fxd_{fs} are fixed costs per day per fattened male and female multiplied by the length of respective fattening period (LF_{ms} and LF_{fs}) and Fx_F are fixed cost per fattened animal. Splitting fixed costs into fixed per animal per day and fixed per animal only is a consequence of the fixed slaughter weights assumed in the model for young animals. In this situation, some costs are affected by the length of the fattening period (labour, machinery, straw and health costs), but others are not. The latter category includes costs due to some health treatments and labour, such as handling of animals when entering and leaving the farm, that are unrelated to the time spent by the animals at the farm.

Costs for cows (C_C) include feeding for cows ($Feed_c$), breeding heifers ($Feed_h$) and calves up to weaning ($Feed_{cal}$), feeding costs during the finishing period of culled heifers and cows ($Feed_{cull}$), dystocia costs ($Dyst$) and other fixed husbandry costs for cows-calves (Fx_c) and heifers (Fx_h):

$$C_c = Feed_c + Feed_h + Feed_{cal} + Feed_{cull} + Dyst + Fx_c + Fx_h \qquad (13)$$

Dystocia costs include veterinary fee, additional labour and increased costs for involuntary culling, whereas the effect of calving difficulties on cows fertility and stillbirth of calves directly affects farm revenues, reducing the number of weaned calves available for

fattening (see equation 1). Dystocia costs are modelled separately for first and later parities (Meijering, 1986) as:

$$Dyst = [\Phi(t_2 - \mu) - \Phi(t_1 - \mu)]c_{diff} + [\Phi(t_3 - \mu) - \Phi(t_2 - \mu)]c_{ces} +$$
$$+ [1 - \Phi(t_3 - \mu)]c_{foet} \tag{14}$$

where $\Phi(t)$ is the cumulative standard density function, $t_i - \mu$ is the distance between mean liability and threshold t_i in units of the standard normal liability scale and $c_{diff}, c_{ces}, c_{foet}$ are the costs due to a difficult calving, cesarean section and foetotomy expressed as additional costs in comparison with an easy calving. Incidence of animals included in the i-1 category of calving score is $\Phi(t_i - \mu) - \Phi(t_{i-1} - \mu)$. The assumed partition of calvings across calving score classes in first and later parities is as in Albera et al. (1999).

Other husbandry costs for cows and heifers (Fx_c and Fx_h), such as machinery, labour, straw for litter, health and insemination fees are treated as fixed per animal.

Depreciation and insurance for housing and machinery, electricity, slurry removal and interest on investments are considered as fixed costs for the farm (C_{FX}).

Variable costs and revenues have been discounted to a 1-year time horizon.

Growth

The model simulates growth of animals on a daily basis.

Growth of calves up to weaning is considered fixed (within sex) and unrelated to dam's milk production and growth after weaning.

Post-weaning gain of young animals during the fattening period is assumed linear; for heifers a growth rate 20% lower than that of young bulls is assumed.

Dynamics of growth of breeding heifers after weaning and cows is considered non-linear. A growth curve for Piemontese breeding females is modelled using age and weight data of 1078 females collected in 27 farms over a 1-year period (Albera, unpublished) according to the Von Bertalanffy curve (Brown et al., 1976).

Within age class of heifers and cows a linear growth is considered. Weight of a breeding female in age class i at day y is:

$$Weight_{iy} = Weight_{i0} + Dg_i \times y \tag{15}$$

where $Weight_{i0}$ is weight at the lower bound of age class i provided by the Von Bertalanffy curve and Dg_i is the linear daily gain (g/d) within age class i computed as the difference between the weights provided by the Von Bertalanffy curve at the upper and lower bound of the age class i, divided by the length (days) of the age class i.

Linear growth within age class is then expressed as a proportion of young bulls growth in order to relate growth and mature weight of breeding females to growth of fattened animals.

Heifers culled in age class 3 and culled cows are sold for slaughter after a finishing period of 150 d. During this finishing period, a linear growth of animals not dependent on previous growth is modelled.

Fleshiness

The evaluation of carcass conformation based on a scoring system is not adopted for the commercialization of Piemontese slaughter animals. Animals for slaughter are marketed on the basis of a price per kg of live weight provided by professional operators through the assessment of muscular development on live animals. For selection purposes, muscular development of animals is evaluated by trained classifiers through a 9 point linear scoring of live fleshiness in six regions of the body (Albera et al., 2001). An equation, expressing market value of young bulls as a function of live fleshiness scores, is developed through linear multiple regression using a dataset of 673 young bulls both scored for live fleshiness by classifiers and evaluated for market value by professional butchers (Albera, unpublished). This equation is also used to estimate market values of heifers and culled cows. The relationship between changes in muscular development and changes in body composition has been ignored due to the lack of specific information relating the evaluation of conformation on live animals with lean tissue deposition.

Energy intake

A daily simulation of feeding of animals has been adopted in the model.

Daily net energy intake of young bulls during the fattening period is modelled according to the equation provided by Bittante (1984) considering maintenance and growth requirements.

Daily net energy requirements for fattened and breeding heifers are simulated by developing equations from INRA standards for late mature beef breeds based on live weight and daily gain of animals (Geay and Micol, 1988; Troccon et al., 1988).

Energy intake of cows is modelled considering maintenance, gestation and lactation requirements. Maintenance requirements are merely a function of live weight (Petit, 1988).

Gestation and lactation requirements are modelled considering the proportion of cows calving per year (*Fert*). Energy requirements for gestation are accounted for in the last 4 months before parturition considering an average birth weight of 45 kg for Piemontese calves. Data on milk production of Piemontese cows reported by Berra and Di Stasio (1995) are used in the model.

During the finishing period, fixed energy intakes proportional to live weight and growth rate are assumed for culled heifers and cows according to fattening requirements of suckler cows (Geay and Micol, 1988).

Feeding costs result from multiplying simulated net energy requirements times the cost per unit of energy.

Economic values

Economic values are derived at a fixed number of cows per herd with the aim of profit maximization (Groen, 1989c), corresponding to individual producer interest (Harris, 1970). The economic value of a trait is defined as the change in profit due to a marginal change in genetic merit of the trait, while keeping other traits constant. For each trait, computations are made by comparing the farm profit after a 1% increase in the mean of the trait to the farm profit in the base situation. For categorical traits, CE_h and CE_c, the mean of the normal underlying distribution are increased (Meijering, 1986).

Economic values are derived for different levels of performance, management and economic conditions in order to appraise their sensitivity to production circumstances. Trait levels, price of slaughter animals, energy and labour costs and herd size are either increased or decreased by 10% and economic values are estimated again under the new situations.

The effect of a limitation on input (energy) or on output (kg of live weight) of the farm is also evaluated. When a limitation exists, the size of the system is defined by the size of

the quota and the improvement of economic efficiency of production will result in a decrease of the number of cows (Groen, 1989b). Therefore, economic values under input and output limitations are derived by rescaling the number of cows after a marginal increase in the level of a trait in order to fit the size of the quota.

Biological values

Biological values reflect the contribution of traits to the improvement of efficiency of energy utilization. In this study efficiency of live weight production is expressed as:

$$EE_{LW} = T_{NE} / T_{LW} \ \text{(kJ NE/kg live weight)} \tag{16}$$

where T_{NE} and T_{LW} are respectively total net energy consumption and total live weight production (young bulls, heifers and culled cows) of the herd. Difference between energy utilization efficiency after and before a marginal increase of traits level provides estimates of biological values.

Results and discussion

Model outputs

Table 2 reports the economic and biological efficiency indicators according to different production levels for traits. Simulated profit of the farm is positive. Feeding costs account for nearly 50% of total costs of the farm. In the simulated farm all feeds are assumed to be purchased from the market and crop production and related labour requirements are not modelled; as a consequence, labour costs are moderate. When considering only the fattening sector, the most important cost is due to the purchase of weaned calves at cost price from the suckler cows part of the farm. Cost price of a weaned calf from the model is around 60% of the market price. Hence, a separate modelling of suckler cows and fattening sector is expected to lead to different results in terms of profit and to affect the estimated economic values of traits (Jiang et al., 1998).

Table 2. Simulated economic and biological parameters in relation to production levels.

Parameter	Basic	DG[†] -10%	DG[†] +10%	FLESH[†] -10%	FLESH[†] +10%	CE[†] -10%	CE[†] +10%	CI[†] -10%	CI[†] +10%
Annual profit									
Herd (€)	17702	16413	18765	16277	19127	16101	19908	23276	13141
Per cow (€)	354.0	328.3	375.3	325.5	382.5	322.0	378.2	465.5	262.8
Per young bull (€)	632.0	595.8	662.7	597.5	666.6	608.8	649.3	685.2	580.2
Per slaughter heifer (€)	501.0	474.8	521.8	472.4	529.5	477.6	518.3	554.1	448.7
Cost prices									
Weaned calf (€)	580.6	575.3	585.9	587.9	573.3	600.5	565.8	545.0	614.9
Young bull (€*kg live weight^{-1})	2.12	2.18	2.07	2.13	2.11	2.16	2.09	2.03	2.21
Slaughter heifer (€*kg live weight^{-1})	2.55	2.60	2.50	2.57	2.53	2.60	2.51	2.43	2.67
Net energy consumption									
Cow (GJ*year^{-1})	17.75	16.87	18.64	17.75	17.75	17.73	17.77	18.30	17.30
Per weaned calf (GJ)	16.55	15.73	17.37	16.55	16.55	16.77	16.40	15.64	17.43
Young bull (MJ*kg live weight^{-1})	23.50	25.31	21.87	23.50	23.50	23.50	23.50	23.50	23.50
Slaughter heifer (MJ*kg live weight^{-1})	25.46	27.05	24.13	25.46	25.46	25.46	25.46	25.46	25.46

† DG = daily gain; FLESH = live fleshiness scores; CE = calving ease; CI = calving interval.

Changes in the level of studied traits cause either a linear (FLESH) or non-linear (DG, CE CI) modification of the simulated economic parameters.

A higher DG level improves biological efficiency of beef production of slaughter animals, but also increases the energy consumption of suckler cows due to the correlated response on cow body weight. Reduction of CI leads to an increase of energy intake of suckler cows per year due to higher gestation and lactation requirements. A similar effect is observed when CE in increased. However, considering weaned calves production, improvement of both traits has a positive effect on biological efficiency due to a decreased energy consumption per weaned calf produced.

Economic values in the base situation and for alternative trait levels

Economic values for beef traits in the base situation and for alternative production levels are reported in Table 3. Because fixed slaughter weights are assumed, a marginal increase of DG reduces the length of the fattening period and variable costs and fixed costs per animal per day. The economic value of DG is positive because the reduction of the costs for the fattening process due to a 1% marginal increase of the trait exceeded the increased feeding costs for breeding heifers and cows. When DG level is increased by 10% the economic value is unchanged compared to the base situation. In this case the use of production factors saved by the improvement in growth performance is limited by the availability of calves born at the farm, as the purchase of weaned calves is not typical for Piemontese farms. Bekman and Van Arendonk (1993) reported a sensitivity of economic value of DG to growth level for Black and White beef bulls slaughtered at fixed a weight, whereas Hirooka et al. (1998) found a non-linear reduction of economic value at a high level of growth.

Fertility of the herd slightly affects the economic value of DG as a consequence of the relation between the number of calves available for fattening and CI.

In general, the economic value of FLESH is quite stable at different levels of other traits showing a limited sensitivity only to changes in DG and CI levels, due to the effect that these traits exert respectively on the length of the fattening period and on the number of calves fattened per year. The economic value of FLESH is linearly dependent on the level of muscular development. This is expected because a linear relationship between FLESH and price per kg of live weight of slaughter animals is modelled and the effect exerted by changes in the body composition on nutrients requirements for different levels of FLESH is not considered.

Studies dealing with the evaluation of conformation on live animals in the frame of breeding goal definition could not be found in literature, because marketing of slaughter animals is often based on carcass traits. Amer et al. (1997) showed that the economic value of carcass conformation score was dependent on the level of conformation, when a non-linear pricing scheme of carcasses related to conformation was applied and reported a higher economic value for poor conformation level. Hence, the sensitivity of economic values of conformation traits to their level depends on the payment system for carcass or live slaughter animals used in the market.

Table 3. Economic values of beef production traits in the base situation and for alternative production levels ($€*year^{-1}*cow^{-1}*trait\ unit^{-1}$)[a].

Traits[†]	Basic	DG		FLESH		CE$_h$		CE$_c$		CI	
		-10%	+10%	-10%	+10%	-10%	+10%	-10%	+10%	-10%	+10%
DG	0.20	0.20	0.20	0.19	0.20	0.20	0.20	0.20	0.19	0.23	0.17
FLESH	57.01	56.02	57.97	51.30	62.70	57.00	57.00	57.00	56.72	61.72	53.14
CE$_h$	0.57	0.57	0.56	0.57	0.57	0.70	0.39	0.56	0.57	0.58	0.56
CE$_c$	1.99	2.05	1.93	2.01	1.97	1.99	1.99	3.16	1.01	2.21	1.81
CI	-2.60	-2.52	-2.67	-2.54	-2.65	-2.60	-2.60	-2.53	-2.65	-3.14	-2.11

[†] *DG = daily gain; FLESH = live fleshiness scores; CE$_h$ = calving ease in heifers; CE$_c$ = calving ease in cows; CI = calving interval.*

[a] *g/d for DG, point (scale 1-9) for FLESH, 1% in the liability scale for CE, 1 d for CI.*

Despite the reduced incidence of dystocia in second and later parities cows compared with heifers, the economic value of CE_c is nearly four times as high as that of CE_h. This is not in agreement with results obtained by Albera et al. (1999), who computed the economic losses due to dystocia, in terms of stillbirth and reduced fertility, considering the market price of newborn calves. In this paper an integrated system is modelled where the fattening process determines directly the value of calves born. Calving problems limit the number of animals available for fattening per year and the income of the farm. Given the herd composition, the majority of calves are born from cows. Furthermore, economic losses due to involuntary culling caused by calving problems are higher in cows. Cows have a lower value for slaughter compared with first parity cows which are usually culled under three years of age. As a consequence, the improvement of CE_c has a stronger impact on farm profit than that of CE_h. The model used for this study assumes that birth weights of calves are unaffected by changes in the level of CE, even though there is evidence of a negative genetic correlation between these traits (Koots et al., 1994). Calving ease score is a complex trait, resulting from a combination of birth weight, gestation length, calf and dam ability. Furthermore, direct and maternal genetic components showing a negative correlation (Carnier et al., 2000) regulate the expression of CE. The economic value of direct and maternal components of CE is the same. Differences in the economic importance between direct and maternal effects arise from rate and time of expression of superior genes as accounted for when computing cumulative discounted expressions (Dekkers, 1994). Similarly to other studies (Munoz-Luna et al.*,* 1988; Koots and Gibson, 1998b), the economic values of CE_h and CE_c are sensitive to the level of dystocia. Compared with the base situation, a 10% increase of calving difficulties (i.e. a 10% decrease of CE) increases the economic values of CE_h and CE_c of 23 and 59% respectively. A corresponding decrease of calving difficulties has opposite effects: the economic importance of CE_c is markedly reduced due to the occurrence of nearly all calvings in unassisted or easy categories of calving.

In this study CI is adopted as an overall measure of reproductive efficiency of females including oestrus detection, pregnancy rate and gestation length which is assumed as unchanged when CI level is improved. The economic value of CI exhibits a negative sign because of the effect that an additional day in the interval exerts on the economic efficiency of the herd. Estimated value is dependent on the level of fertility in the herd as found by other authors (Groen et al., 1994; Amer et al., 1996). However, differently from other

studies, the economic importance of CI increases when the fertility level is higher than that in the base situation as a consequence of an increased availability of calves for fattening. The economic value of CI shows also a moderate sensitivity to DG and FLESH: the benefit of an improved CI is better exploited when the fattening period is shorter and the value of slaughter animals is higher due to their muscular development.

Economic values for alternative production circumstances

The effect of alternative production circumstances on the economic values of traits is reported in Table 4. Changes in the herd size do not affect the estimates of economic values, but only determine changes in the profit of the herd. The cost of energy affects the economic values of CI in a moderate way. The improvement of CI increases the nutrient requirements for gestation and lactation. Therefore when feeding costs are higher the economic value of this trait is reduced.

Table 4. Economic values of beef production traits for the base situation and for alternative production circumstances ($€*year^{-1}*cow^{-1}*trait\ unit^{-1}$)[a].

Production circumstance	Change	Traits[†]				
		DG	FLESH	CE_h	CE_c	CI
Basic		0.20	57.01	0.57	1.99	-2.60
Number of cows	-10%	0.20	57.01	0.57	1.99	-2.60
	+10%	0.20	57.01	0.57	1.99	-2.60
Cost of energy unit	-10%	0.20	57.00	0.57	1.99	-2.69
	+10%	0.19	57.01	0.56	1.99	-2.51
Price of slaughter animals	-10%	0.18	57.00	0.55	1.99	-2.28
	+10%	0.21	57.01	0.58	1.99	-2.92
Cost of labour	-10%	0.19	57.01	0.57	1.99	-2.62
	+10%	0.20	57.00	0.57	1.99	-2.58
Fixed output (live weight)		0.11	57.01	0.38	1.46	-1.09
Fixed input (energy)		0.12	57.01	0.47	1.73	-1.70

[†] *DG = daily gain; FLESH = live fleshiness scores; CE_h = calving ease in heifers; CE_c = calving ease in cows; CI = calving interval.*
[a] *g/d for DG, point (scale 1-9) for FLESH, 1% in the liability scale for CE, 1 d for CI.*

Changes in the market price of slaughter animals have no effect on the economic value of FLESH due to the assumed linear relationship between this trait and the price per kg of live weight. A higher availability of calves and a shortening in the fattening period due to improvement of CI and DG have a major impact on the economic efficiency of the herd when the value of slaughter animals is increased.

The effect of changes in labour cost on the economic values is negligible for all traits.

Setting a limitation on total production of live weight causes a dramatic reduction of economic values of all traits but FLESH. Decrease in the economic values ranges from 58% for CI to 27% for CE_c. A limitation in the energy input produces a similar effect. Compared with the situation with output limitation, decline of the economic value is lower for DG, CE_h, CE_c and CI (13 to 40%). Again, economic value of FLESH is unchanged.

The insensitivity to energy input limitations shown by FLESH depends on the lack of specific relationship between muscular development and energy consumption assumed in the model. At the same way, the limitation on the output does not affect the economic value of FLESH because this trait is related to the value but not to the amount of live weight production.

Limitations in the input or output affect the use of saved production factors through the improvement of economic efficiency of production. With a quota, saved production factors get an alternative use which is external to the system. If the system is making profit, the value of production factors for the use within the system generally exceeds their market (alternative) value and economic values are usually influenced by this difference (Groen, 1989b). A moderate sensitivity of economic values to input or output restrictions is generally reported in literature for beef cattle (Koots and Gibson, 1998b; Simm et al., 1986) as a consequence of the small profit generated by the system.

In this study, the simulated farm has a moderate positive profit, which increases when farm size increases. The reduction of the economic values observed when limitations are set indicates that the alternative use of saved production factors has a low profitability.

Brascamp et al. (1985) suggested to derive economic values in a situation of zero profit, including the 'normal' profit among costs. They argued that the occurrence of a high profit is not realistic in a long term period for a sector, because it leads to an increase of production and, as a consequence, to a reduction of price. However, the pure competitive nature of the agricultural sector is questionable and probably is more realistic to consider

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different farms having different production costs and also differences in term of profit (Groen, 1989c).

Biological values

It has been argued that biological efficiency instead of economic efficiency should be used in defining breeding objectives in order to assure sustainability of genetic improvement (Dickerson, 1982). However, difficulties in the expression of costs and revenues in terms of energy or protein consumption and lack of differentiation between values of products when biological efficiency is considered make this criterion unable to describe the overall objective of the producers (Harris and Newman, 1994). In general, even if future economic conditions can be difficult to foresee, the definition of the breeding goal according an economic criterion allows a more complete description of the production system by taking into account also non-food costs (Dickerson, 1970; Goddard, 1998).

Table 5. Biological values of beef production traits for the base situation and for alternative production levels (KJ NE*kg live weight^{-1}*trait unit^{-1})[a].

Production level	Change	Traits[†]				
		DG	FLESH	CE_h	CE_c	CI
Basic		-1.23	0	-7.50	-21.18	47.35
DG	-10%	-1.00	0	-7.22	-20.40	44.96
	+10%	-1.39	0	-7.74	-21.89	49.54
FLESH	-10%	-1.23	0	-7.50	-21.18	47.35
	+10%	-1.23	0	-7.50	-21.18	47.35
CE_h	-10%	-1.21	0	-9.85	-21.25	47.56
	+10%	-1.25	0	-4.54	-21.12	47.17
CE_c	-10%	-1.13	0	-7.61	-47.17	47.62
	+10%	-1.30	0	-7.35	-11.35	47.15
CI	-10%	-2.03	0	-6.72	-20.41	47.58
	+10%	-0.49	0	-8.27	-21.85	45.02

[†] *DG = daily gain; FLESH = live fleshiness scores; CE_h = calving ease in heifers; CE_c = calving ease in cows; CI = calving interval.*
[a] *g/d for DG, point (scale 1-9) for FLESH, 1% in the liability scale for CE, 1 d for CI.*

In this study the derivation of biological values of traits is aimed to appraise whether the improvement of the economic efficiency, adopted as a goal in the definition of the breeding objective, also leads to the improvement of the biological efficiency. Estimates of biological values of studied traits are presented in Table 5 for the base situation and for alternative trait levels. Negative signs in the biological values mean a better efficiency of production due to a decrease in the net energy consumption. Four traits, DG, CE_h, CE_c and CI, exhibit biological values which agree with economic values, indicating that improvement of these traits is also expected to increase the efficiency in the energy utilization. Differently from other traits, FLESH has a biological value of zero, because in the model this trait is considered independent from energy utilization.

When trait levels are changed, biological values of CE_h, CE_c and CI exhibit a sensitivity similar to that of corresponding economic values; the biological value of DG is sensitive to fertility levels and, differently from economic values, also to growth and CE_c levels showing higher values when these traits are increased.

Conclusions

This study is a first step in the definition of an economic selection index for the Piemontese breed. The derived economic values indicate that considered traits are relevant for the economic efficiency of the Piemontese beef cattle farms. The influence of alternative production levels is moderate and affect especially CE_h and CE_c. For these traits the profit function appears to be non-linear and dependent on the level of population mean.

Therefore, adjustments in the economic values might be needed when the average performance in these traits differs from the basic situation as a result of undergoing selection. The economic values of all traits are robust to changes in the price of products or production-factors indicating that the breeding goal is unaffected by uncertainty in anticipating future prices. However, the introduction of a limitation either on the energy input or live weight output has a massive impact on the absolute and relative levels of economic values; as a consequence the breeding objective should be redefined when a quota system is applied.

The use of biological instead of economic efficiency would lead to set up a different breeding goal. In general the use of economic values is preferred in the definition of

breeding goals, but is important to recognize that in this study the improvement in the economic efficiency also leads to improved efficiency in energy utilization in most of the traits.

When several traits are included in the breeding goal differences in the rate and time of expressions of genetic superiority in the progeny of selected animals can arise between traits. This occurs for beef production traits and reproductive traits and also for the direct and maternal components of calving ease. Therefore, the derivation of the cumulative discounted expressions is a further step to be accomplished in order to determine the relative emphasis of the traits in the breeding goal.

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Chapter 3

Genetic parameters for direct and maternal calving ability over parities in Piedmontese cattle

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Abstract

Estimates of heritabilities and genetic correlations for calving ease over parities were obtained for the Italian Piemontese population using animal models. Field data were calving records of 50,721 first- and 44,148 second-parity females and 142,869 records of 38,213 cows of second or later parity. Calving ability was scored in five categories and analyzed using either a univariate or a bivariate linear model treating performance over parities as different traits. The bivariate model was used to investigate the genetic relationship between first and second or between first and third parity calving ability. All models included direct and maternal genetic effects which were assumed to be mutually correlated. (Co)variance components were estimated using restricted maximum likelihood procedures.

In the univariate analyses, the heritability for direct effects was 0.19 ± 0.01, 0.10 ± 0.01, and 0.08 ± 0.004 for first, second, and second and later parities, respectively. The heritability for maternal effects was 0.09 ± 0.01, 0.11 ± 0.01, and 0.05 ± 0.01, respectively. All genetic correlations between direct and maternal effects were negative, ranging from -0.55 to -0.43. Approximated SE of genetic correlations between direct and maternal effects ranged from 0.041 to 0.062. For multiparous cows, the fraction of total variance due to the permanent environment was greater than the maternal heritability.

With bivariate models, direct heritability for first parity was smaller than the corresponding univariate estimate, ranging from 0.18 to 0.14. Maternal heritabilities were slightly higher than the corresponding univariate estimates. Genetic correlation between first and second parity was 0.998 ± 0.00 for direct effects and 0.913 ± 0.01 for maternal effects. When the bivariate model analyzed first and third parity calving ability, genetic correlation was 0.907 ± 0.02 for direct effects and 0.979 ± 0.01 for maternal effects. Residual correlations were low in all bivariate analyses, ranging from 0.13 for analysis of first and second parity to 0.07 for analysis of first and third parity.

In conclusion, estimates of genetic correlations for calving ease in different parities obtained in this study were very high but variance components and heritabilities were clearly heterogeneous over parities.

Keywords: Beef Cattle, Calving Ease, Double Muscling, Genetic Parameters

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Introduction

The ability to calve easily is an important trait in beef cattle affecting profitability of herds, animal welfare, and acceptability of the production system by the consumer (Jarrige and Beranger, 1992). Maternal effects influence biological aspects of calving ability (Philipsson, 1976; Meijering, 1986). As a consequence, models used in the genetic analysis of calving ease include two random effects: a sire and a maternal grandsire effect (sire-mgs model) or a calf and a dam effect (animal model). In most literature reports, these effects exhibit antagonistic genetic relationships, which is a complicating factor in optimizing breeding strategies.

Rates of dystocia are higher in first parity than in later parities, probably as a result of different relative sizes of the dam and the calf (Meijering, 1986). Some authors hypothesized heterogeneity of (co)variance components by parity for dystocia to be due to differences in the genetic nature of calving ease and suggested that calving ability in first and later parities should be considered as different traits (Cue and Hayes, 1985; Weller et al., 1988). Reported estimates of genetic correlations for calving ability between heifers and adult cows in Holstein cattle differ largely but models were limited either to sire (direct) or to grandsire (maternal) effects (Thompson et al., 1981; Cue and Hayes, 1985; Weller et al., 1988).

In Italy, the Piemontese breed is actively selected for beef production characteristics. The muscular hypertrophy of the breed is due to a specific mutation in the myostatin coding sequence (Grobet et al., 1998). In the last decade concern about calving ability has increased, due to a gradual increase in incidence of dystocia (ANABORAPI, 1997). Young bulls, selected for beef production ability at the end of a performance testing program, are progeny tested for calving ease on mature cows to reduce risk of dystocia in heifers. Currently, there is no defined selection and mating strategy for calving ease, and required estimates of genetic parameters for direct and maternal calving ability over different parities in Piemontese or other double-muscled cattle breeds are not available in literature. The objective of this study was to estimate genetic parameters for calving ease in Piemontese breed using an animal model and treating calving ease in different parities as different traits.

Material and Methods

Field Data

Data used in this study were calving records of Piemontese heifers and cows that calved from January 1989 to December 1997. Calving ability was scored by farmers and recorded by technicians visiting the farms monthly. Since 1989, calving ability has been scored in five categories: 1 (unassisted delivery), 2 (assisted easy calving), 3 (assisted difficult calving), 4 (cesarean section), and 5 (foetotomy).

A calving record consisted of calf and dam identity codes, date of calving, sex of the calf, birth date and parity of the dam, herd code, and calving ease category. No informations on the genotype at the myostatine locus were available for this study. Pedigree records were extracted from the official breed registry files of the Italian Piemontese cattle association.

The original data were partitioned into three data sets: data set 1 for heifers (first parity records), data set 2 for second parity records, and data set 3 for second and later parities records. A total of 68,278 first, 56,113 second, and 159,829 second and later parities calving records were available before data editing. Records with incomplete informations, records collected in very small herds (less than five calving records over nine years), and records pertaining to twinning births were discarded. Pedigree checks were made to discard records of calves with missing sire, dam, maternal grandsire, and(or) granddam. To form the inverse of the relationship matrix, the pedigree was traced back for as many generations as available. A minimum of two calving records was required for each cow in data set 3. After edits, the numbers of records were 50,721, 44,148, and 142,869 for data sets 1, 2, and 3, respectively. Characteristics of data sets after editing procedures are in Table 1. Most sires had less than 11 calves and a great number of maternal grandsires had less than 10 daughters. The percentages of cows for whom calving ease was recorded at their birth were 10.5, 8.8, and 22.6% for data set 1, 2, and 3, respectively.

Two additional data sets were created to investigate the relationship between first and later parities calving ability. Such analyses were performed either considering females that calved in the same herd as a heifer and as a second parity cow, or females that calved in the same herd as a heifer and as a third parity cow. There were 34,476 heifers (139,723 animals in pedigree file) with also a second parity record and 23,869 heifers (105,833 animals in pedigree file) with a third parity record in the same herd.

Table 1. Summary of data by parity after editing procedures

Item	Parity		
	First	Second	Second and later
	No.		
Calving records	50,721	44,148	142,869
Herds	2,054	2,115	2,108
Male calves	25,858	22,530	73,147
Female calves	24,863	21,618	69,722
Cows	50,721	44,148	38,213
Cows with own birth record	5,328	3,866	8,626
Sires[a]	3,661	3,428	4,051
With 1 to 10 calves	2,872	2,632	2,285
With 11 to 25 calves	545	528	780
With 26 to 50 calves	153	161	484
With 51 to 100 calves	38	50	259
With 101 to 200 calves	22	28	143
With more than 200 calves	31	29	101
Maternal grandsires	3,794	3,743	4,319
With 1 to 10 daughters	2,904	2,884	3,564
With 11 to 25 daughters	575	588	538
With 26 to 50 daughters	183	163	131
With 51 to 100 daughters	59	49	38
With 101 to 200 daughters	39	29	26
With more than 200 daughters	34	30	23
Records in pedigree file	142,951	131,005	206,827

[a]*Sires being also maternal grandsires were 2,394, 1,990, and 1,803 for first, second, and second and later parities, respectively.*

Linear Models

The method of choice in the analysis of categorical traits is the threshold model. However, in this study preference was given to the use of linear models because routines for estimating the genetic correlation between calving ability of heifers and that of cows by a bivariate threshold animal model with both direct and maternal effects included were not readily available. To avoid use of different methodologies, also univariate analyses were performed with linear models.

Variance components were estimated using the software package VCE (Neumaier and Groeneveld, 1998) which uses restricted maximum likelihood implementing a quasi-Newton optimization algorithm on the Cholesky factor of the covariance matrices.

Model 1 was used in univariate analysis of heifers and second parity cows calving ability:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_d u_d} + \mathbf{Z_m u_m} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of calving ease scores, $\mathbf{b}$ is a vector of non-genetic fixed effects, $\mathbf{u_d}$ is an unknown random vector of additive direct genetic effects, $\mathbf{u_m}$ is an unknown random vector of additive maternal genetic effects, and $\mathbf{e}$ is an unknown random vector of residuals. $\mathbf{X}, \mathbf{Z_d}$, and $\mathbf{Z_m}$ are known incidence matrices relating calving ease records to $\mathbf{b}$, $\mathbf{u_d}$, and $\mathbf{u_m}$, respectively. The distributional assumption about the random terms of the model was :

$$[\mathbf{u'_d}\ \mathbf{u'_m}\ \mathbf{e'}\ \mathbf{y'}]' \sim \mathbf{N}([0'\ 0'\ 0'\ (\mathbf{Xb})']', \Phi_1)$$

where

$$\Phi_1 = \begin{vmatrix} \mathbf{A}\sigma_d^2 & \mathbf{A}\sigma_{dm} & 0 & \mathbf{AZ'_d}\sigma_d^2 \\ \mathbf{A}\sigma_{dm} & \mathbf{A}\sigma_m^2 & 0 & \mathbf{AZ'_m}\sigma_m^2 \\ 0 & 0 & \mathbf{I}\sigma_e^2 & \mathbf{I}\sigma_e^2 \\ \mathbf{Z_d A}\sigma_d^2 & \mathbf{Z_m A}\sigma_m^2 & \mathbf{I}\sigma_e^2 & \mathbf{V}_1 \end{vmatrix},$$

$\sigma_{\mathbf{d}}^2$ is the additive direct genetic variance, $\sigma_{\mathbf{dm}}$ is the additive genetic covariance between direct and maternal effects, $\sigma_{\mathbf{m}}^2$ is the additive maternal genetic variance, $\sigma_{\mathbf{e}}^2$ is the residual variance, $\mathbf{A}$ is the numerator of Wright's relationship matrix, and

$$\mathbf{V}_1 = \mathbf{Z_d} \mathbf{A} \mathbf{Z_d'} \sigma_{\mathbf{d}}^2 + \mathbf{Z_m} \mathbf{A} \mathbf{Z_m'} \sigma_{\mathbf{m}}^2 + (\mathbf{Z_d} \mathbf{A} \mathbf{Z_m'} + \mathbf{Z_m} \mathbf{A} \mathbf{Z_d'}) \sigma_{\mathbf{dm}} + \mathbf{I} \sigma_{\mathbf{e}}^2 .$$

Model 2 was based on Model 1 and was extended to include permanent environment effects in univariate analysis of second and later parities cows data (data set 3) :

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_d} \mathbf{u_d} + \mathbf{Z_m} \mathbf{u_m} + \mathbf{Z_p} \mathbf{u_p} + \mathbf{e}$$

where $\mathbf{y}, \mathbf{b}, \mathbf{u_d}, \mathbf{u_m}, \mathbf{e}, \mathbf{X}, \mathbf{Z_d}$, and $\mathbf{Z_m}$ are defined as in Model 1, $\mathbf{u_p}$ is a random vector of unknown permanent environment effects, and $\mathbf{Z_p}$ is a known incidence matrix relating calving ease scores to $\mathbf{u_p}$. The distributional assumption about the random terms of Model 2 was :

$$[\mathbf{u_d'} \ \mathbf{u_m'} \ \mathbf{p'} \ \mathbf{e'} \ \mathbf{y'}]' \sim \mathbf{N}([\mathbf{0'} \ \mathbf{0'} \ \mathbf{0'} \ \mathbf{0'} \ (\mathbf{Xb})']', \Phi_2)$$

where

$$\Phi_2 = \begin{vmatrix} \mathbf{A}\sigma_{\mathbf{d}}^2 & \mathbf{A}\sigma_{\mathbf{dm}} & 0 & 0 & \mathbf{A}\mathbf{Z_d'}\sigma_{\mathbf{d}}^2 \\ \mathbf{A}\sigma_{\mathbf{dm}} & \mathbf{A}\sigma_{\mathbf{m}}^2 & 0 & 0 & \mathbf{A}\mathbf{Z_m'}\sigma_{\mathbf{m}}^2 \\ 0 & 0 & \mathbf{I}\sigma_{\mathbf{p}}^2 & 0 & \mathbf{Z_p'}\sigma_{\mathbf{p}}^2 \\ 0 & 0 & 0 & \mathbf{I}\sigma_{\mathbf{e}}^2 & \mathbf{I}\sigma_{\mathbf{e}}^2 \\ \mathbf{Z_d}\mathbf{A}\sigma_{\mathbf{d}}^2 & \mathbf{Z_m}\mathbf{A}\sigma_{\mathbf{m}}^2 & \mathbf{Z}\sigma_{\mathbf{p}}^2 & \mathbf{I}\sigma_{\mathbf{e}}^2 & \mathbf{V}_2 \end{vmatrix},$$

$\sigma_{\mathbf{d}}^2, \sigma_{\mathbf{dm}}, \sigma_{\mathbf{m}}^2, \sigma_{\mathbf{e}}^2$, and $\mathbf{A}$ are defined as in Model 1, $\sigma_{\mathbf{p}}^2$ is the permanent environment variance, and

$$\mathbf{V}_2 = \mathbf{Z_d A Z_d'} \sigma_d^2 + \mathbf{Z_m A Z_m'} \sigma_m^2 + (\mathbf{Z_d A Z_m'} + \mathbf{Z_m A Z_d'})\,\sigma_{dm} + \mathbf{Z_p Z_p'} \sigma_p^2 + \mathbf{I} \sigma_e^2\,.$$

Model 3 was a bivariate animal model used to investigate the relationship between first and later parities calving ability :

$$
\left|\begin{array}{c} \mathbf{y^h} \\ \mathbf{y^c} \end{array}\right| =
\left|\begin{array}{cc} \mathbf{X^h} & 0 \\ 0 & \mathbf{X^c} \end{array}\right|
\left|\begin{array}{c} \mathbf{b^h} \\ \mathbf{b^c} \end{array}\right| +
\left|\begin{array}{cccc} \mathbf{Z_d^h} & 0 & \mathbf{Z_m^h} & 0 \\ 0 & \mathbf{Z_d^c} & 0 & \mathbf{Z_m^c} \end{array}\right|
\left|\begin{array}{c} \mathbf{u_d^h} \\ \mathbf{u_d^c} \\ \mathbf{u_m^h} \\ \mathbf{u_m^c} \end{array}\right| +
\left|\begin{array}{c} \mathbf{e^h} \\ \mathbf{e^c} \end{array}\right|
$$

where $\mathbf{y^h}$ ($\mathbf{y^c}$) is a vector of observations on calving ability of heifers (cows), $\mathbf{b^h}$ ($\mathbf{b^c}$) is a vector of fixed effects for heifers (cows), $\mathbf{u_d^h}$ ($\mathbf{u_d^c}$) is an unknown random vector of additive direct genetic effects for heifers (cows), $\mathbf{u_m^h}$ ($\mathbf{u_m^c}$) is an unknown random vector of additive maternal genetic effects for heifers (cows), and $\mathbf{e^h}$ ($\mathbf{e^c}$) is a random vector of residuals for heifers (cows) data, and $\mathbf{X^h}, \mathbf{X^c}, \mathbf{Z_d^h}, \mathbf{Z_d^c}, \mathbf{Z_m^h}$, and $\mathbf{Z_m^c}$ are known matrices. All random effects were assumed to be normally distributed with null means and variance structure :

$$
\mathbf{V}\left|\begin{array}{c} \mathbf{u_d^h} \\ \mathbf{u_d^c} \\ \mathbf{u_m^h} \\ \mathbf{u_m^c} \end{array}\right| =
\left|\begin{array}{cccc}
\sigma_d^{2(h)} & \sigma_d^{(hc)} & \sigma_{dm}^{(h)} & \sigma_{dm}^{(hc)} \\
\sigma_d^{(hc)} & \sigma_d^{2(c)} & \sigma_{dm}^{(ch)} & \sigma_{dm}^{(c)} \\
\sigma_{dm}^{(h)} & \sigma_{dm}^{(ch)} & \sigma_m^{2(h)} & \sigma_m^{(hc)} \\
\sigma_{dm}^{(hc)} & \sigma_{dm}^{(c)} & \sigma_m^{(hc)} & \sigma_m^{2(c)}
\end{array}\right| \otimes \mathbf{A}\,,
$$

$$
\mathbf{V}\left|\begin{array}{c} \mathbf{e^h} \\ \mathbf{e^c} \end{array}\right| =
\left|\begin{array}{cc} \sigma_e^{2(h)} & \sigma_e^{(hc)} \\ \sigma_e^{(hc)} & \sigma_e^{2(c)} \end{array}\right| \otimes \mathbf{I}\,,
$$

where $\sigma_d^{2(h)}$ ($\sigma_d^{2(c)}$) is the additive direct genetic variance for heifers (cows) calving ability, $\sigma_m^{2(h)}$ ($\sigma_m^{2(c)}$) is the additive maternal genetic variance for heifers (cows) , $\sigma_{dm}^{(h)}$ ($\sigma_{dm}^{(c)}$) is the additive genetic covariance between direct and maternal effects in heifers

(cows), $\sigma_{\mathbf{d}}^{\mathbf{(hc)}}$ is the covariance between heifers and cows additive direct genetic effects, $\sigma_{\mathbf{m}}^{\mathbf{(hc)}}$ is the covariance between heifers and cows additive maternal genetic effects, $\sigma_{\mathbf{dm}}^{\mathbf{(hc)}}$ is the covariance between heifers additive direct and cows additive maternal genetic effects, $\sigma_{\mathbf{dm}}^{\mathbf{(ch)}}$ is the covariance between cows additive direct and heifers additive maternal genetic effects, $\sigma_{\mathbf{e}}^{2\,\mathbf{(h)}}$ ($\sigma_{\mathbf{e}}^{2\,\mathbf{(c)}}$) is the residual variance for calving ability in heifers (cows), and $\sigma_{\mathbf{e}}^{\mathbf{(hc)}}$ is the residual covariance between calving ease records of an animal calving as a heifers and as a cow, $\mathbf{I}$ is an identity matrix , and $\otimes$ denotes the Kronecker product (Searle, 1982).

Heritability for direct and maternal effects was computed as

$$\mathbf{h}_{\mathbf{d}}^2 = \sigma_{\mathbf{d}}^2 \,/(\sigma_{\mathbf{d}}^2 + \sigma_{\mathbf{m}}^2 + \sigma_{\mathbf{dm}} + \sigma_{\mathbf{e}}^2)$$

and

$$\mathbf{h}_{\mathbf{m}}^2 = \sigma_{\mathbf{m}}^2 \,/(\sigma_{\mathbf{d}}^2 + \sigma_{\mathbf{m}}^2 + \sigma_{\mathbf{dm}} + \sigma_{\mathbf{e}}^2)\text{, respectively.}$$

Standard errors for estimates of heritabilities were approximated using the following formula (Falconer, 1989) :

$$\mathrm{SE}_{\hat{h}^2} = 4 * \sqrt{\frac{2\,(1-t)^2\,[1+(k-1)\,t]^2}{k\,(k-1)\,(s-1)}}$$

where t is the intraclass correlation approximated by $h^2/4$ for paternal half-sib estimates, k is the average number of offspring per sire, and s is the number of sires. Standard errors for maternal heritability estimates were computed using the same formula but replacing s with the number of maternal grandsires and k with the average number of daughters per maternal grandsire. Approximated SE for estimates of genetic correlations were computed using the following formula (Falconer, 1989) :

$$\mathrm{SE}_{\hat{r}_g} = \frac{1 - \hat{r}_g^2}{\sqrt{2}} \sqrt{\frac{\mathrm{SE}_{\hat{h}_1^2}\,\mathrm{SE}_{\hat{h}_2^2}}{\hat{h}_1^2\,\hat{h}_2^2}}$$

where $\hat{r}_g$ is the estimated genetic correlation, $\hat{h}_1^2$ and $\hat{h}_2^2$ are the estimates of heritability and $SE_{\hat{h}_1^2}$ and $SE_{\hat{h}_2^2}$ are the SE of the estimated heritabilities.

Nongenetic Fixed Effects

Nongenetic effects considered in mixed models were from preliminary analyses based on generalized linear model procedure of SAS (SAS, 1990).

Due to small herd size, the effect of herd and year-season of calving were fitted as separate effects in univariate analysis of heifers and second parity cows calving ability and in all bivariate models. For these analyses, the effect of a herd was then assumed to be unchanged across years and seasons. Two seasons of calving, from November to April and from May to October, were defined.

Besides herd and year-season effects, univariate analysis of heifers and second parity calving ability (Model 1) considered the effect of the sex of the calf, age at parturition of the dam (eight classes from 21 to 37 mo in heifers, 15 classes from 31 to 67 mo in second parity cows), and the interaction between sex of the calf and age class of the dam.

Model 2 accounted for the fixed effects of herd-year-season, age at calving within parity, and sex of the calf. Due to the presence of small sized herds, the herd-year-season effect was defined using a flexible classification system. For a small herd (less than 60 calving observations over nine years), the herd-year-season class included all available observations for that herd, (i.e., actually it was a herd effect). For a herd of medium size (from 60 to 120 calving records in nine years), the herd-year-season class included all calvings that occurred in a year (herd-year effect). Only for herds having more than 120 calving observations in nine years two seasons of calving were considered : from November to April and from May to October (herd-year-season effect).

Nongenetic effects included in bivariate models (Model 3) were the same effects as considered in the univariate analysis of heifers calving scores. Because different calvings for a cow occurred in different years and seasons originating calves that might have differed in sex, models used in bivariate analysis had unequal design with respect to the definition of year-season and sex-age of the dam effects for different parities of the same cow.

Results and discussion

Univariate Analyses

Frequency distribution of calving ease categories by parity is reported in Table 2. Incidence of dystocia (assisted difficult calvings, cesarean sections and foetotomy) was twice as high in heifers as in later parity cows and cesarean sections were carried out three times more frequently when heifers calved. Occurrence of calving difficulties in second parity cows was similar to that in older cows.

Table 2. Frequency of calving scores categories by parity

Calving score category	Parity		
	First	Second	Second and later
	%		
1 Unassisted	11.6	18.0	20.9
2 Assisted easy	60.0	68.6	66.0
3 Assisted difficult	14.7	9.2	8.9
4 Cesarean section	13.1	4.1	4.0
5 Foetotomy	0.6	0.2	0.3

Estimates of variance components and related parameters obtained performing univariate analysis of calving records are presented in Table 3. Estimated heritabilities and correlations were within the range of values reported in literature and approximated SE of parameters were rather low.

Analysis of calving ability for Piemontese cows yielded variance estimates which were consistently smaller than those obtained for heifers. Particularly, variance and heritability of direct genetic effects exhibited a marked decrease from analysis of heifers to analysis of cows. For second parity females, direct and maternal variances were similar and corresponding heritabilities were comparable in size to the heritability of maternal effects

for heifers. When variance components were estimated after pooling records of second and later parities, heritabilities were even smaller than those computed using only records of second parity females. Magnitude of maternal heritability was halved when compared to the corresponding estimate obtained for heifers or cows at second calving.

Table 3. Estimates of variance components and related parameters (± approximated SE) obtained in univariate analysis of calving ability by parity

Parameter[a]	Parity		
	First	Second	Second and later
σ_d^2	0.1260	0.0500	0.0300
σ_m^2	0.0610	0.0551	0.0185
σ_{dm}	-0.0420	-0.0291	-0.0101
σ_p^2	-	-	0.0228
σ_e^2	0.5159	0.4070	0.3167
h_d^2	0.191 ± 0.011	0.104 ± 0.010	0.079 ± 0.004
h_m^2	0.092 ± 0.009	0.114 ± 0.010	0.049 ± 0.011
r_{dm}	-0.479 ± 0.041	-0.553 ± 0.045	-0.427 ± 0.062
c^2	-	-	0.060

[a]*The term σ_d^2 is the genetic variance of direct effects, σ_m^2 is the genetic variance of maternal effects, σ_{dm} is the genetic covariance between direct and maternal effects, σ_p^2 is the permanent environment variance, σ_e^2 is the residual variance, h_d^2 is the heritability for direct effects, h_m^2 is the heritability for maternal effects, r_{dm} is the genetic correlation between direct and maternal effects, and c^2 is the fraction of total variance due to the permanent environment.*

Differences in magnitude of heritabilities over parities are likely associated with higher incidence of difficult calvings experienced by heifers than by cows. A possible

biological explanation for such differences considers the interaction between the size of the calf and the area of the pelvic inlet of the dam. Meijering (1986) pointed out that the ratio between calf size and pelvic dimensions is more critical in heifers than in cows. Indeed, the area of the pelvic inlet increases with parity relatively more than calf size does (Menissier, 1975), causing a more favorable ratio of calf size to pelvic dimensions in cows than in heifers.

Differences in variance observed between heifers and cows might also be explained by a higher fraction of dams being relatively immature at first calving than at later calvings.

Gregory et al. (1995a, 1995b) reported estimates of direct heritability for calving ease in beef cattle to be higher for calves born to 2-yr-old dams than for calves born to older dams. Also most studies dealing with calving ease scores in dairy cattle reported higher estimates of heritability for heifers than for cows.

Studies by Thompson et al. (1981) and Groen et al. (1998) reported additive genetic variance due to direct effects to be greater than that due to maternal effects in Holstein Friesian cattle but Cue and Hayes (1985) and Cue et al. (1990) found direct genetic variance in Holstein heifers to be slightly smaller than the maternal variance. In beef cattle, Varona et al. (1999) used an animal model to estimate variance components for calving difficulties in American Gelbvieh first-parity females obtaining a larger variance for direct than for maternal effects. With no partitioning of data by parity, Trus and Wilton (1988) obtained estimates of direct variance and heritability which were greater than maternal estimates for Angus, Hereford, and Charolais but smaller for Simmental. Also Burfening et al. (1981) estimated for 2-yr-old Simmental heifers a maternal component larger than the variance due to direct effects. In a comprehensive review, Koots et al. (1994a) averaged estimates of heritability for calving ability (percentage of unassisted calvings) over a number of studies obtaining a value of direct heritability higher for cows than for heifers and a value of maternal heritability which was identical for cows and heifers. Most studies that defined calving ease as a binary trait obtained similar results (Weller et al., 1988; Lin et al., 1989).

Estimated heritabilities obtained in the present study were lower than those reported by Trus and Wilton (1988) for five beef breeds but were higher than the estimates computed by Kemp et al. (1988) in Simmental cattle or by McGuirk et al. (1998) for some beef breeds used in crossbreeding with Holstein cows. Factors which might explain such differences include breed, trait definition, model, and method of estimation. Koots et al. (1994a, 1994b) showed that differences in estimated parameters for calving ability across studies were

significantly affected by breed, country in which the animals were raised, data origin (experimental or field data), and sex. Because they are estimates of variance prior to selection, animal model estimates of heritability are expected to be higher than estimates based on sire or sire-maternal grandsire models. Koots et al. (1994a) pointed out that lack of selection, insufficient pedigree informations for tracing back to the unselected base population or better statistical models fitted may cause failure of animal models in yielding estimates greater than those from other estimation methods. Varona et al. (1999) used both a linear and a threshold animal model to estimate variance components for calving difficulties in American Gelbvieh cattle. They considered only first-parity calving ability and obtained heritabilities very similar to the ones estimated for Piemontese heifers in the present study.

Estimated genetic covariances between direct and maternal genetic effects were negative both for heifers and cows. As a consequence, all genetic correlations between direct and maternal effects were negative ranging from -0.43 to -0.55. These results indicate that antagonistic relationships exist between calving ease as a trait of the calf and as a trait of the dam and that, from a genetic point of view, female calves born more easily are expected to exhibit greater difficulties when giving birth as dams. A number of studies reported antagonistic genetic relationships between direct and maternal effects on calving ease in dairy (Dwyer et al., 1986; Groen et al., 1995) and beef cattle (Burfening et al., 1981; Trus and Wilton, 1988; Cubas et al., 1991). Few studies have reported null or synergic relationships between direct and maternal effects. Groen et al. (1998) estimated a large positive genetic correlation from calving data with no directional mating of virgin heifers to low risk sires and Cue and Hayes (1985) reported a correlation close to zero for multiparous cows.

Biological aspects related to the relationship between direct and indirect effects on calving ease have been discussed by Thompson et al. (1981) and Meijering (1986), who suggested that female calves of small size are likely to be born easily but may experience more difficult calvings when giving birth because of reduced pelvic dimensions. Kriese et al. (1994) estimated additive genetic correlation between male d-320 pelvic measurements and calving ease scores of 2-yr-old females from data of nine breeds and three composite populations and suggested that an increase of pelvic measurements in male contemporaries would result in a small to moderate decrease of calving difficulty in females. Robinson (1996) reported that negative estimates of correlations between direct and maternal effects might be a result of ignoring variation due to sire by herd or sire by year interaction. In this

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study, due to the specific structure of the data, investigating the effects of such interactions was not feasible.

Evidence of antagonistic genetic relationships between direct and maternal effects is a complicating factor in optimization of breeding strategies for calving ability. Genetic gain resulting from selection on merit for only one component of calving ability, for example direct effects, can be counteracted to some extent by the negative response in the maternal calving ability. Further, direct and maternal effects exhibit differences in rate and timing of expression of genetic superiority of sires which give raise to differences in relative economic values. Hence, selection for both genetic components of calving ability using an index with proper weighing of direct and maternal effects (Dekkers, 1994) seems a good strategy.

The current selection goal for the Piemontese population is the improvement of the efficiency of beef production which is dependent, to a large extent, on growth rate and muscularity. A number of study reported antagonistic genetic relationships between calving ability and beef production traits.The expected biological consequence of selection on direct merit for calving ability is a reduction of birth weight, which is reported to be correlated to growth rate, and calf conformation. Hence, definition of breeding strategies for the Piemontese population will require also knowledge of the relationships between direct and maternal calving ability and traits which define efficiency of beef production.

Bivariate Analyses

Genetic and residual variance components obtained with bivariate models treating calving ability for different parities as different traits are presented in Tables 4 and 5, respectively. Because such analyses were very demanding in terms of both computing time and memory requirements, they were limited to heifers that also had a second calving record or to heifers that calved also as a third parity cow in the same herd. This constraint reduced the size of the analysis and computer memory requirements.

With the only exception of direct genetic variance for first calving ability, bivariate analysis of first and second parity calving ability yielded additive genetic variances that were greater than the corresponding estimates obtained in univariate analyses. Genetic covariances between direct and maternal effects were more negative than the corresponding univariate estimates for both first and second parity calving ability.

Table 4. Estimates of genetic (co)variances obtained with bivariate models treating calving ability in different parities as different traits

Parameter[a]	Bivariate model	
	First and second parity	First and third parity
$\sigma_d^{2(h)}$	0.1080	0.0774
$\sigma_m^{2(h)}$	0.0738	0.0525
$\sigma_d^{2(c)}$	0.0538	0.0468
$\sigma_m^{2(c)}$	0.0599	0.0197
$\sigma_{dm}^{(h)}$	-0.0459	-0.0311
$\sigma_{dm}^{(c)}$	-0.0321	-0.0206
$\sigma_d^{(hc)}$	0.0761	0.0546
$\sigma_m^{(hc)}$	0.0607	0.0315
$\sigma_{dm}^{(hc)}$	-0.0443	-0.0251
$\sigma_{dm}^{(ch)}$	-0.0317	-0.0254

[a]*The term $\sigma_d^{2(h)}$ is the direct genetic variance for first parity, $\sigma_m^{2(h)}$ is the maternal genetic variance for first parity, $\sigma_d^{2(c)}$ is the direct genetic variance for second or third parity, $\sigma_m^{2(c)}$ is the maternal genetic variance for second or third parity, $\sigma_{dm}^{(h)}$ is the genetic covariance between direct and maternal effects for first parity, $\sigma_{dm}^{(c)}$ is the genetic covariance between direct and maternal effects for second or third parity, $\sigma_d^{(hc)}$ is the genetic covariance between direct effects for first parity and direct effects for second or third parity, $\sigma_m^{(hc)}$ is the genetic covariance between maternal effects for first parity and maternal effects for second or third parity, $\sigma_{dm}^{(hc)}$ is the genetic covariance between direct effects for first parity and maternal effects for second or third parity, and $\sigma_{dm}^{(ch)}$ is the genetic covariance between direct effects for second or third parity and maternal effects for first parity.*

Table 5. Estimates of residual (co)variances and correlations obtained with bivariate models treating calving ability in different parities as different traits

Parameter[a]	Bivariate model	
	First and second parity	First and third parity
$\sigma_e^{2(h)}$	0.4662	0.4654
$\sigma_e^{2(c)}$	0.4120	0.3797
$\sigma_e^{(hc)}$	0.0556	0.0255
$r_e^{(hc)}$	0.1269	0.0707

[a]*The term $\sigma_e^{2(h)}$ is the residual variance for first parity, $\sigma_e^{2(c)}$ is the residual variance for first parity, $\sigma_e^{(hc)}$ is the residual covariance between first and second or third parity, and $r_e^{(hc)}$ is the residual correlation between first and second or third parity.*

Estimates of first parity genetic variances from bivariate analysis of first and third parity calving ability were smaller than the univariate estimates whereas the genetic covariance between direct and maternal effect for first parity was, in absolute value, lower than the one estimated in the univariate analysis. Estimates of residual correlations were 0.13 for first and second parity and 0.07 for first and third parity. Even though magnitude of residual correlations was small, not accounting for such correlations in bivariate models would have biased the estimated genetic correlations.

Heritabilities and genetic correlations obtained using bivariate models are presented in Table 6. Analysis of first and second parity calving ability yielded a value of first-parity direct heritability that was slightly smaller than that obtained with univariate models, but other heritability estimates were slightly greater than univariate estimates. Changes in heritability estimates were not a result of consistent changes in either the estimated genetic and(or) residual variance components. Direct heritability for first parity was 0.14 when the bivariate model was applied to first and third parity calving perfomance. This value was much lower than the corresponding estimate obtained with the univariate model. This difference might be partly explained by the change in the data structure that occurred when the bivariate analysis was performed and that was more important for analysis of first and third parity records than for analysis of first and second parity calving ability.

Table 6. Estimates of heritabilities and genetic correlations (± approximated SE) obtained with bivariate models treating calving ability in different parities as different traits

Parameter[a]	Bivariate model	
	First and second parity	First and third parity
$h_d^{2(h)}$	0.179 ± 0.013	0.137 ± 0.016
$h_m^{2(h)}$	0.123 ± 0.012	0.093 ± 0.015
$h_d^{2(c)}$	0.109 ± 0.012	0.110 ± 0.015
$h_m^{2(c)}$	0.121 ± 0.012	0.046 ± 0.014
$r_{dm}^{(h)}$	-0.514 ± 0.044	-0.487 ± 0.074
$r_{dm}^{(c)}$	-0.566 ± 0.050	-0.676 ± 0.078
$r_d^{(hc)}$	0.998 ± 0.000	0.907 ± 0.016
$r_m^{(hc)}$	0.913 ± 0.012	0.979 ± 0.007
$r_{dm}^{(hc)}$	-0.551 ± 0.042	-0.643 ± 0.078
$r_{dm}^{(ch)}$	-0.503 ± 0.055	-0.511 ± 0.077

[a]*The term $h_d^{2(h)}$ is the direct heritability for first parity, $h_m^{2(h)}$ is the maternal heritability for first parity, $h_d^{2(c)}$ is the direct heritability for second or third parity, $h_m^{2(c)}$ is the maternal heritability for second or third parity, $r_{dm}^{(h)}$ is the genetic correlation between direct and maternal effects for first parity, $r_{dm}^{(c)}$ is the genetic correlation between direct and maternal effects for second or third parity, $r_d^{(hc)}$ is the genetic correlation between direct effects for first parity and direct effects for second or third parity, $r_m^{(hc)}$ is the genetic correlation between maternal effects for first parity and maternal effects for second or third parity, $r_{dm}^{(hc)}$ is the genetic correlation between direct effects for first parity and maternal effects for second or third parity, and $r_{dm}^{(ch)}$ is the genetic correlation between direct effects for second or third parity and maternal effects for first parity.*

Selection decisions are not expected to be influenced by differences in parameter estimates obtained with univariate and bivariate models.

Again, genetic correlations between direct and maternal effects were negative and very similar to those obtained in the univariate analysis.

Genetic correlations between direct effects for first and second parity and for first and third parity were 0.998 and 0.907, respectively, suggesting that the same genes are involved in the control of direct calving ability of heifers and cows. Thus, ranking of sires for direct effects on cows calving ability is expected to be very similar to that based on calving ability of heifers. Because of a lower heritability, accuracy of genetic evaluations of sires for direct effects based on calvings of cows is smaller than that of evaluations based on calving ability of heifers.

Progeny testing of young bulls for calving ability on adult females, which is widely practiced in the Piemontese population to reduce risks of calving problems in heifers, might have affected the estimate of the genetic correlation between direct effects over parities obtained in this study. Such matings are expected to reduce incidence of difficult calvings and, as a consequence, to reduce variance of calving ease in heifers. This has an immediate effect on correlations among parities.

Estimates of genetic correlations between parities are scarce and limited to sire models. Thompson et al. (1981) and Cue and Hayes (1985) investigated the relationship between direct effects for Holstein heifers and cows using a linear sire model and reported a correlation between direct effects of 0.84 and 0.995, respectively. Lower estimates were obtained by Cue (1990) who investigated genetic aspects of calving ease over parities in Ayrshire cattle. Weller et al. (1988) reported low correlations between first and later parity sire evaluations for calving ease in Israeli Holsteins either when using a threshold or a linear model analysis.

Genetic relationships between maternal effects over parities were high and correlations ranged from 0.91 for first and second parity to 0.98 for first and third parity. These results suggest that prediction of breeding values for maternal effects using performance of first-parity daughters would provide at an earlier stage the same information provided by daughters at later calvings.

Implications

Animal model estimates of genetic parameters for calving ease have been obtained for the Piemontese population taking into account both direct and maternal effects. These estimates are the basis for the genetic evaluation of calving ability for the Italian Piemontese population. Values of heritability and genetic variances obtained in this study indicate that reducing calving difficulties by selection is feasible. Genetic correlations for calving ability in different parities were very high, but variance components and heritabilities were heterogeneous between heifers and cows. This implies that evaluation of sires for calving ease should be performed treating calving ability in first parity as a different trait from calving ability in later parities. Specific breeding strategies, taking into account the genetic antagonism between direct and maternal effects and involving also beef production traits, need to be identified.

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Chapter 4

Genetic parameters for daily live-weight gain, live fleshiness and bone thinness in station-tested Piemontese young bulls

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Abstract

Estimates of genetic parameters for beef production traits were obtained for Piemontese cattle. Data were from 988 young bulls station-tested from 1989 till 1998. Bulls entered the station at 6-8 weeks of age and, after an adaptation period of 3 months, were tested for growth, live fleshiness and bone thinness. Length of test was 196 days. Growth traits considered were gain at farm, gain during the adaptation period, gain on test and total gain at the station. Six different fleshiness traits and bone thinness were scored on live animals at the end of the test using a linear system. Live evaluations of fleshiness were adjusted for the weight at scoring in order to provide an assessment of conformation independent of body size. Genetic parameters were estimated using animal models.

Heritability of live-weight gain ranged from 0.20 in the adaptation period to 0.60 for total gain at the station. Genetic correlations between gains at station in different periods were high (from 0.63 to 0.97). Residual correlation between gain during the adaptation period and gain during test was negative, probably due to the occurrence of compensatory growth of animals.

Live fleshiness traits and bone size were of moderate to high heritability (from 0.34 to 0.55) and highly correlated indicating that heavy muscled bulls also have thin bones. Accuracy of breeding values and therefore response to selection were improved by multiple trait analysis of live fleshiness traits and bone thinness.

Overall weight gain at station had a moderate negative genetic correlation with all live fleshiness traits and bone thinness (from -0.11 to -0.39).

Introduction

The Piemontese is the most important Italian beef breed. The high specialization of this breed is related to the segregating muscular hypertrophy due to a specific mutation in the myostatin coding sequence (McPherron and Lee, 1997; Grobet et al., 1998).

The current breeding goal for the Piemontese breed is the improvement of beef production efficiency and the reduction of dystocia. Selection is performed in two stages: male calves are performance tested for beef production traits at a central station and young bulls selected after performance testing are then progeny tested for direct and maternal calving ease on the basis of birth and calving performance of their progeny (Carnier et al., 2000). The objective of performance testing in the Piemontese breed is the evaluation of young bulls for growth rate, live fleshiness and bone thinness.

Assessment of fleshiness on live animals is a simple method to evaluate carcass quality and, unlike methods requiring slaughtering, can be applied to potential breeding animals. Compared with progeny testing for carcass traits, live evaluations have the advantage of being inexpensive and of allowing a significant reduction of the generation interval in breeding schemes.

Kallweit (1976), Jansen et al. (1985) and Renand (1985) showed that evaluations of fleshiness on live animals by trained operators provided reliable indications of carcass conformation and could be efficiently used to improve carcass composition and value.

Genetic aspects of traits related to growth have been widely studied both in field and station conditions and genetic parameters for these traits are generally well known.

Likewise, estimates of (co)variance components and genetic parameters for traits related to muscular development, like live fleshiness or muscularity scores, have been obtained in some studies (Mohiuddin, 1993; Miglior et al., 1994; Schafer et al., 1998), but the definition and recording of such traits are not consistent across studies. In recent years Mohiuddin (1993) and Koots et al. (1994a and 1994b) published extensive literature reviews of genetic parameters for beef traits. Nevertheless, few investigations have been conducted on double-muscled cattle (Gengler et al., 1995) and no previous estimates for beef production traits are available for the Piemontese breed.

This study aimed to estimate heritabilities and genetic correlations for daily live-weight gain, live fleshiness and bone thinness in station-tested Piemontese young bulls and

to compare accuracy of estimated breeding values obtained for these traits using single and multiple trait models.

Material and Methods

Animal management

Performance testing of Piemontese bulls is carried out at the central station of the Italian Piemontese Cattle Association (ANABORAPI) located in Carrù, Italy.

Every month 14 male calves (6 to 8 wk old) enter the station and form groups of contemporary animals. Entry of calves forming a contemporary group is over a period of 7 to 10 days. Before the beginning of the test animals go through a quarantine and a subsequent adaptation period of 3 months. During this period health tests are carried out. Animals are given a milk replacer, concentrate and hay. At the end of the adaptation period, 10 out of the 14 calves showing better performance, are admitted to the performance testing program.

Performance testing is over a period of 196 days, between 4.5 and 11.5 months of age. Animals are kept in loose housing in groups of five and are given restricted concentrate based on maize meal, soya-bean meal, barley meal, sugar beet pulp, wheat bran, molasses, mineral and vitamin supplements and hay *ad libitum*.

Traits

Live-weight records of 988 young bulls station-tested from 1989 till 1998 were available for this study. Traits considered in the analysis were daily gain at farm from birth to the admission at the station (daily gain at farm, FG), daily gain during the adaptation period (AG), daily gain on test (TG), overall daily gain at the station (OG).

Because repeated observations on weight were available for each calf since the adaptation period, AG, TG and OG were computed as the slope of the individual linear regression of weight on the age at weighing. FG was computed relating the difference between the weight at the admission and estimated birth weight to the age at the admission. The weight at admission is recorded after all the calves forming a contemporary group have entered the station.

A linear system to score live fleshiness of young bulls has been adopted at the genetic station since 1991. As a consequence, records were available only for 692 out of the 988 young bulls. All bulls were scored independently by three classifiers using a 1 to 9 points scale at the end of the test (10 animals in the first contemporary group have been scored by only two classifiers). One record consisted of the average of the three scores given by the classifiers. Traits considered were withers width (from above, WW), shoulder muscularity (by sideview, SM), loins width (from above, LW), loins thickness (by sideview, LT), thigh muscularity (by rear view, TM), thigh profile (by sideview, TP). Also bone thinness (thickness of the shin-bone, BT) was evaluated using the same scoring system.

The lower values of the scale indicate reduced muscular development and thick bones, whereas higher values are related to strong muscular masses and thin bones. Number of records and descriptive statistics for the traits are reported in Table 1.

Models

To investigate the effects to be fitted in the models for estimation of genetic parameters, preliminary analyses were carried out through general linear model procedure of Statistical Analysis Systems Institue (SAS, 1989). Effects tested were contemporary group on test (year-month effect), age of the calf at the entrance and parity of the dam. For live fleshiness traits and bone thinness also the linear and quadratic effects of the weight of the bulls at scoring were also considered in preliminary analyses. These effects were included in models for estimating (co)variance components when they were strictly environmental, i.e. when the amount of variation of a trait accounted for by the weight at scoring was not trivial and the genetic correlation between weight at scoring and a fleshiness trait was low.

A preliminary multivariate analysis considering all live fleshiness traits, bone size and weight at scoring was carried out in order to achieve estimates of the genetic correlations among these traits.

The data structure did not allow fitting the effect of the classifier in the model, beacause individual classifiers have changed over time; therefore, the average of the scores given by the three classifiers was used in the model for live fleshiness traits and bone thinness. The effect of the herd of origin of the calves could not be considered in the model due to the small number of observations per herd

Table 1. Number of records and descriptive statistics for traits

Trait[†]	No.	Mean	s.d.	Minimum	Maximum
Growth traits					
FG (kg/day)	988	0.859	0.238	0.229	1.914
AG (kg/day)	988	0.818	0.155	0.260	1.467
TG (kg/day)	988	1.400	0.350	0.978	1.849
OG (kg/day)	988	1.258	0.113	0.935	1.602
WA (kg)	988	97.1	16.98	53	160
WBT (kg)	988	163.6	22.42	100	232
WET (kg)	988	434.2	37.03	326	568
Live fleshiness traits[‡]					
Withers width	692	6.22	0.97	3.00	8.60
Shoulder muscularity	692	6.10	0.92	3.50	8.60
Loins width	692	6.04	0.83	3.60	8.60
Loins thickness	692	6.22	0.86	3.50	9.00
Thigh muscularity	692	6.21	1.06	3.60	9.00
Thigh profile	692	6.05	0.96	3.60	9.00
Bone thinness§	692	5.69	0.67	3.30	8.00

[†] *FG = daily gain before the admission to the station; AG = daily gain during the adaptation period; TG = daily gain during the test; OG = overall daily gain at the station; WA = weight at the admission at the station; WBT = weight at the beginning of the test; WET = weight at the end of the test.*
[‡] *Nine-point scale (1 = reduced development, 9 = high development).*
§ *Nine-point scale (1 = thick, 9 = thin).*

(Co)variance components were estimated using animal model restricted maximum likelihood procedures (REML) (Neumaier and Groenevelt, 1998). A multivariate analysis was performed in order to investigate the relationships among growth traits. For one trait the model was:

$$Y_{ijkl} = CG_i + P_j + a_k + e_{ijkl}$$

where Y_{ijkl} is an observation on the trait, CG_i is the fixed effect of the contemporary group of tested animals i (1, …, 109), P_j is the fixed effect of the parity of the dam j (1, …, 4), a_k is the random additive genetic effect and e_{ijkl} is a random residual.

Four classes of parity of the dam were defined: first, second, third to seventh, higher than seventh.

Live fleshiness traits and bone thinness were analysed using both univariate and multivariate models. For a fleshiness trait the model was

$$Y_{ijkl} = CG_i + P_j + bW_{ijkl} + a_k + e_{ijkl}$$

where Y_{ijkl} is an observation on the trait, CG_i, P_j, a_k and e_{ijkl} keep the meaning formerly specified, W_{ijkl} is the weight of the bull at scoring and b is the linear regression coefficient of the trait on W.

The model used for bone size was similar to the model for analysing growth traits.

Estimated breeding values and approximated accuracies for live fleshiness traits and bone thinness were predicted using estimated genetic parameters. Accuracy and estimated breeding values resulting from single trait analysis were compared with those obtained with multiple trait models using correlation analysis (SAS, 1989).

Relationships between OG, live fleshiness traits and bone size were studied using records of 692 bulls and a multivariate model. Fixed and random effects for each trait were the same as specified in previous analyses. Hence models were unequal for different traits.

In all multivariate analyses the variance structure assumed for the random components of the model was $G \otimes A$ and $E \otimes I$ where G and E are the (co)variance matrices for the additive genetic and the residual effect, respectively, A is the numerator of Wright's relationship matrix, I is an identity matrix of proper order and $\otimes$ denotes the Kronecker product operator.

All known relationships were considered in the analyses (on average 4.5 generations of ancestors) and two genetic phantom groups, one for unknown male and the other for unknown female parents, were defined. The total number of animals in the pedigree file was 6036 and 5098 for analysis of daily gain and other traits, respectively. Analyses on live

fleshiness traits were also performed considering reduced pedigree information, limiting the pedigree file to three or two generations of ancestors.

Nearly 10% of bulls tested at the station were also sires of other tested bulls. Pedigree information for the tested bulls is reported in Table 2.

Table 2. Pedigree information for the tested bulls

Type of relationship	No. of animals
Sire-son pairs	394
Fullsibs	4
Paternal halfsibs	743
Maternal halfsibs	93

Results

Genetic parameters for daily live-weight gains

Heritabilities, genetic and residual correlations and their standard errors for daily gains are in Table 3. Heritability of AG (0.20) was half that of FG. Heritability of TG was considerably higher than that of pre-weaning growth. OG exhibited a value of heritability the same as that of TG.

Genetic correlations between AG, OG and TG were high ranging from 0.63 to 0.97. FG showed a moderate genetic relationship with AG and even smaller genetic correlations with gains realized in later stages. Residual correlations in general were lower than corresponding genetic correlations.

As expected, FG exhibited small residual correlations with traits measured at the station. All residual correlations for the other growth traits were positive with the exception of AG and TG, which showed a slightly negative correlation.

Table 3. Estimates of heritabilities (diagonal), genetic (above diagonal) and residual (below diagonal) correlations for growth traits obtained with multiple trait analysis[†]

Trait‡	FG	AG	TG	OG
FG	0.428	0.384	0.121	0.173
AG	-0.074	0.201	0.631	0.798
TG	0.145	-0.102	0.595	0.970
OG	0.180	0.420	0.816	0.603

[†] *Standard errors of heritabilities ranged from 0.001 to 0.004. Standard errors of genetic correlations ranged from 0.001 to 0.006. Standard errors of residual correlations ranged from 0.001 to 0.003.*
‡ FG = daily gain before the admission to the station; AG = daily gain during the adaptation period; TG = daily gain during the test; OG = overall daily gain at the station.

Genetic parameters for live fleshiness and bone thinness

Genetic correlations between live fleshiness traits and body weight at scoring were rather low, whereas bone thinness exhibited a negative genetic correlation with body weight (Table 4). As a consequence, the effect of body weight was not accounted for in models

used for analysis of bone thinness. The linear effect of body weight was significant (P < 0.001) for all live fleshiness traits and correcting for this effect markedly increased the coefficient of determination of the model (Table 4).

Table 4. Genetic correlations (r_g) of live fleshiness traits and bone thinness with body weight at scoring and effect of correcting for body weight at scoring on R^2 of models

Trait		R^2	
	r_g	Not correcting for	Correcting for
Withers width	0.18	0.184	0.340
Shoulder muscularity	0.11	0.167	0.340
Loins width	-0.06	0.260	0.396
Loins thickness	0.25	0.298	0.435
Thigh muscularity	-0.02	0.218	0.330
Thigh profile	-0.18	0.228	0.307
Bone thinness	-0.66	-	-

Estimated genetic parameters for live fleshiness traits and bone thinness obtained with single trait and multiple trait models are presented in table 5 and 6. With single trait analysis heritabilities ranged from 0.26 to 0.53. When using multivariate model corresponding values were on average 18% higher and standard errors of estimates were considerably lower than those obtained with univariate models.

All genetic correlations among live fleshiness traits were very high ranging from 0.74 to 0.98. Also the genetic relationships between bone thinness and live fleshiness traits were positive (from 0.52 to 0.63).

Estimates of residual correlations were substantial for all traits, but their values were lower than those of genetic correlations.

Estimates of genetic parameters were affected by the amount of pedigree information available. When the pedigree file was restricted to two or three generations of ancestors resulting estimates of additive genetic variances were higher, residual variances were lower and the convergence process to get solutions was slower than in the corresponding analysis with complete pedigree information (data not shown).

Table 5. Estimates of additive genetic (σ_a^2) and residual (σ_e^2) variance components and heritabilities (h^2) for live fleshiness traits and bone thinness obtained with single trait analysis[†]

Trait	σ_a^2	σ_e^2	h^2
Withers width	0.319	0.387	0.452
Shoulder muscularity	0.344	0.310	0.526
Loins width	0.216	0.265	0.448
Loins thickness	0.123	0.357	0.257
Thigh muscularity	0.317	0.550	0.366
Thigh profile	0.214	0.514	0.294
Bone thinness	0.161	0.253	0.389

[†] *Standard errors of heritabilities ranged from 0.041 to 0.11.*

Table 6. Estimates of heritabilities (diagonal), genetic (above diagonal) and residual (below diagonal) correlations for live fleshiness traits and bone thinness obtained with multiple trait analysis[†]

Trait[‡]	WW	SM	LW	LT	TM	TP	BT
WW	0.534	0.978	0.904	0.790	0.739	0.818	0.631
SM	0.668	0.546	0.931	0.883	0.800	0.870	0.558
LW	0.379	0.361	0.530	0.906	0.871	0.845	0.596
LT	0.408	0.396	0.647	0.335	0.818	0.821	0.516
TM	0.551	0.677	0.450	0.479	0.448	0.961	0.568
TP	0.421	0.532	0.422	0.444	0.790	0.412	0.577
BT	0.380	0.486	0.318	0.376	0.464	0.473	0.377

[†] *Standard errors of heritabilities ranged from 0.045 to 0.077. Standard errors of genetic correlations ranged from 0.001 to 0.075. Standard errors of residual correlations ranged from 0.031 to 0.064.*
[‡] *WW = withers width; SM = shoulder muscularity; LW = loins width; LT = loins thickness; TM = thigh muscularity; TP = thigh profile; BS = bone size.*

Relationship among daily gain, live fleshiness and bone thinness

Table 7 shows estimated genetic and residual correlations among OG, live fleshiness traits and bone thinness.

OG exhibited negative genetic correlations with other traits. Magnitude of such correlations was moderate with the exception of those with LW and BT, which showed a rather important negative correlation with OG.

Residual correlations between OG and live fleshiness traits were moderate (from 0.28 to 0.49), whereas it was close to zero between OG and BT.

Table 7. Estimates of genetic (r_g) and residual (r_e) correlations of live fleshiness traits and bone thinness with overall daily gain at the station (OG)[†]

Trait	r_g	r_e
Withers width	-0.106	0.277
Shoulder muscularity	-0.172	0.298
Loins width	-0.373	0.487
Loins thickness	-0.239	0.362
Thigh muscularity	-0.246	0.279
Thigh profile	-0.291	0.295
Bone thinness	-0.393	0.026

[†] *Standard errors of genetic correlations ranged from 0.017 to 0.049. Standard errors of residual correlations ranged from 0.020 to 0.084.*

Discussion

Unitl now , selection of Piemontese young bulls after performance testing was based on phenotypic information only. The aim of this study was to investigate the relationship between beef production traits and to provide genetic parameters required for the implementation of an animal model routine genetic evaluation.

Model

As differences in the estimates of genetic parameters for live fleshiness traits arose when pedigree information was restricted to two or three generations of ancestors, models considering complete relationship matrices among animals were preferred. In this study onlt 30% of the contemporary groups on test were linked directly through the sires. Limiting pedigree information implied a lack of connectedness ampng groups which were linked over 3 generations back. Hagger and Schneeberger (1995) demonstrated that a reduction from all available pedigree information to two generations of ancestors did not affect the estimation of direct and maternal heritabilities and direct-maternal genetic correlation for growth rate from birth to 30 days in sheep. However, for a data structure similar to our study, i.e. with animals distributed through many small contemporary groups or with seasonal use of sires, problems in connectedness between groups might arise. As a result, the robustness of the estimated genetic parameters is affected and consequently biases in genetic evaluations and selection of animals may occur (Kennedy and Trus, 1993). In such a situation, the additive genetic relationship matrix is crucial to provide connection among groups and to increase accuracy of selection. Therefore, few generations of ancestors might not be sufficient to provide ties between different management units.

Meyer (1992) and Waldron et al. (1993) pointed out that maternal effect should be taken into account when estimating genetic parameters for weight gain up to weaning. In this study maternal effects were not included in the model, because animals enter the station at a very young age. Due to data structure, the environmental effect of the herd of origin of the calves was not considered either. Both maternal and herd effect certainly affected the growth realized at the farm and probably also exerted some influences on the gain during the adaptation period. However, due to the very early age at entry to the testing station and to the length of the testing period, their effect on the growth on test is likely to be negligible.

Information on the myostatin locus genotype is not currently available for the Piemontese population, therefore this single gene effect could not be considered in this study.

Growth traits

Similarly to other studies, daily live-weight gain up to weaning showed moderate heritability, indicating a reduced incidence of the genetic component on this growth phase. Koots et al. (1994a) reported a value of 0.29 for heritability of weight gain to weaning,

resulting from a summary of literature estimates obtained in several studies on beef traits. Gregory et al. (1995) for purebred and composite beef populations and Stålhammar and Philipsson (1997) for Swedish beef cattle found heritabilities value for daily weight gain up to weaning ranging from 0.10 to 0.38. Gutierrez et al. (1997) reported a higher value of weight gain to weaning heritability for Asturiana de los Valles cattle.

Gain on test (TG) and total gain at station (OG) were highly heritable and selection on these traits is expected to be effective. In their literature review Koots et al. (1994a) indicated an average value of 0.34 for yearling weight gain and concluded that the origin of data (field or station) did not affect the magnitude of the estimated heritabilities. This was in opposition to the results obtained by Dijkstra et al. (1987) who pointed out that a better control of environmental conditions in central testing test station led to higher estimates of genetic parameters. Liu and Makarechian (1993) in various beef breeds, Miglior et al. (1994) in Limousin and Gengler et al. (1995) in Belgian Blue cattle found heritabilities of postweaning daily weight gain on station-tested animals comparable with that obtained in this study.

Genetic correlations between gains realized on station were high and consistent with literature reports (Koots et al., 1994b), indicating that the same genes are involved in the control of pre-weaning and post-weaning growth. Only the correlations between FG and other gains were small, but estimated birth weight used to calculate FG and the influence of maternal effects such as dam milk production and care might have affected these estimates.

The negative residual correlation between AG and TG suggested that compensatory growth might have occurred. De Rose et al. (1988) reported a negative residual correlation between pre-weaning and post-weaning growth. Hanset et al. (1987), analysing growth of station-tested Belgian Blue bulls from 7 to 12 months of age, reported unfavourable residual correlation between subsequent periods due to measurements errors, differences in fill of the animals and compensatory growth. Carnier (unpublished data) analysed partial growths of Piemontese station-tested bulls using covariance functions. He estimated residual correlations between early and late periods on test ranging from -0.6 to -0.9, evidencing that animals with reduced gain at the beginning of the test tended to have faster growth at later stages.

Live fleshiness and bone size

Evaluation of fleshiness on live animals is aimed to evaluate carcass conformation and dressing proportion of young bulls and should be used as a measure of shape and profile of muscular masses rather than a measure of the amount of muscle. Stålhammar et al. (1997) showed that live evaluations of fleshiness were poor predictors of carcass and muscle weights, which were reliably predicted by body weight of animals, but were good indicators of carcass conformation. It should be noted that, in this study, live fleshiness traits were adjusted for the weight at scoring in order to provide an assessment of carcass conformation independent of body size of bulls.

The genetic independence between live fleshiness traits and weight at scoring reported in this study implied that accounting for the effect of weight when estimating genetic (co)variance components for live fleshiness traits reduced residual variance without any loss in terms of genetic variation. When variance components were estimated without correcting live fleshiness traits for the weight at scoring resulting heritabilities were lower due to an increase in the residual variance (data not reported).

For all live fleshiness traits, multiple trait analysis led to higher additive genetic variances and lower residual variances compared with univariate procedures. As a consequence, estimated heritabilities for these traits were considerably higher with a multiple trait model. Despite the subjective nature of evaluations on live animals, heritabilities were quite high, especially for the traits, like WW, SM and LW that are related to muscular development of the fore body.

Comparing the results of this study with other literature reports is very difficult, due to the different definition of traits used as measures of beef conformation on live animals. Mohiuddin (1993) reported an average value of heritability of 0.24 resulting from a review of literature estimates for muscling score in beef cattle. Miglior et al. (1994) in station-tested Limousin cattle found an estimate of heritability of 0.51 for muscling score, defined as a combination of live evaluation of top line, width and depth of round. Estimates provided by Gregory et al. (1995) for purebred and composite beef cattle breeds, Stålhammar et al. (1997) for Friesian cattle and Schafer et al. (1998) for Limousin and Charolais cattle were lower than those obtained in this study, ranging from 0.20 to 0.35. Gengler et al. (1995) analysed the price per kilogram of liveweight of performance-tested Belgian Blue bulls as a measure of overall muscular development and reported a value of heritability much higher

than those obtained in this study for live fleshiness traits. However, they pointed out that the classifiers' knowledge of the ancestors of bulls might have biased the estimates obtained in their study.

Heritability of bone thinness was similar with single and multiple trait analyses and considerably higher compared with the results of Miglior et al. (1994).

In general live fleshiness traits exhibited tight relationships. Given the magnitude of the genetic correlations, it is questionable whether some of these traits, namely WW and SM in the fore part and TM and TP in the back part of the body, actually were different traits or just provided different measurements of the same trait.

In opposition with the findings of Miglior et al. (1994) in Limousin cattle, bone thinness and live fleshiness traits showed high positive genetic and residual correlations. This implied that young bulls with thinner bones tended to have a better muscular development, which is a favourable relationship for the Piemontese breeding objective.

Estimates of genetic parameters obtained in this study were used to predict breeding values of station-tested bulls for live fleshiness traits and bone thinness and their accuracies.

Correlations between predicted breeding values obtained with single and multiple trait analysis ranged from 0.8 to 0.93; therefore, differences in ranking of bulls are expected. Multiple trait models led to a 13 % average increase in accuracies of predicted breeding values. Such an increase was due to higher heritability values compared to single trait evaluation and to high genetic correlations between live fleshiness traits.

Daily live-weight gain, live fleshiness and bone size

Daily live-weight gain showed moderate unfavourable genetic correlations with live fleshiness traits.

This was a consequence of the definition of live fleshiness as traits unaffected by the size of the bulls, obtained adjusting live evaluations for the weight at scoring. In such a situation young bulls showing high muscular development exhibited slower growth rate.

Also the genetic correlation between OG and BT was negative. Young bulls with faster growth are therefore expected to show thick bones.

Unlike this study, literature estimates for other beef breeds reported no relation (Schafer et al., 1998) or favourable genetic correlation (Miglior et al., 1994; Gengler et al., 1995; Gregory et al., 1995;) between growth traits and muscling score. Inconsistencies

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between this study and the literature reports could be due to them using different ways to evaluate muscular development, different models and breed-specific characteristics.

Results of this study indicated that traits measured during performance testing of Piemontese young bulls are highly heritable. For live fleshiness traits and bone thinness, response to selection should be greater when genetic evaluations are performed using a multivariate model. The negative genetic correlations between daily gain and the other traits should be accounted for in the definition of a selection index.

Optimal selection strategies would require implementing a total merit index for beef production traits considering also calving ease. This implies that relationships between growth and live fleshiness traits and direct and maternal aspects of calving ease need to be studied.

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Chapter 5

Genetic relationships between calving performance and beef production traits in Piemontese cattle

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Abstract

The aim of the study was to obtain estimates of genetic correlations between direct and maternal calving performance of heifers and cows and beef production traits in Piemontese cattle. Beef production traits were daily gain, live fleshiness and bone thinness measured on 1,602 young bulls tested at a central station. Live fleshiness (six traits) and bone thinness were subjectively scored by classifiers using a nine-point linear grid. Data on calving performance were calving difficulty scores (five classes from unassisted to embryotomy) routinely recorded in the farms. Calving performance of heifers and cows were considered different traits. A total of 30,763 and 80,474 calving scores in first and later parities, respectively were used to estimate covariance components with beef traits. Data have been analyzed using bivariate linear animal models including direct genetic effects for calving performance and beef traits and maternal genetic effects only for calving performance. Due to the nature of data structure, involving traits measured in different environments and on different animals, covariances have been estimated mostly through pedigree information. Genetic correlations of daily gain were positive with direct calving performance (0.43 in heifers and 0.50 in cows) and negative with maternal calving performance (-0.23 and -0.28 for heifers and cows, respectively). Live fleshiness traits were moderately correlated with maternal calving performance in both parities, ranging from 0.06 to 0.33. Correlations between live fleshiness traits and direct calving performance were low to moderate and positive in the first parity, trivial in later parities. Bone thinness was negatively correlated with direct calving performance (-0.17 and -0.38 in heifers and cows, respectively) but was positively correlated to maternal calving performance (0.31 and 0.40). Estimated residual correlations were close to zero.

Results indicate that, due to the existence of antagonistic relationships between the investigated traits, specific selection strategies need to be studied.

Introduction

Calving performance is a trait of economic importance in beef cattle production systems (Albera et al., 2004). Biologically, this trait is affected by a direct component, related to calf size, and a maternal component, mainly related to the size of the pelvic area of the dam (Philipsson et al., 1979). Recently, a number of authors provided estimates of genetic parameters for both direct and maternal calving performance in beef cattle (Varona et al., 1999; Carnier et al., 2000) indicating that exploitable genetic variation exists for these traits. Few studies investigated the relationship between calving performance and other traits which are of importance for efficiency of beef production such as growth rate, muscularity and slaughter performance (Renand, 1985a, b; Gregory et al., 1995). Moreover, in most cases only the direct effect of calving performance was considered when estimating covariances with other traits.

The Piemontese is an important breed specialized for beef production in Italy. Piemontese cattle exhibit double muscling (Grobet et al., 1998) and relatively high levels of dystocia. The economic relevance of calving performance and possible unfavourable effects induced by selection for beef production traits suggest to include this trait in the breeding goal of the Piemontese population. Current breeding goals include daily gain, live fleshiness, bone thinness, direct and maternal calving performance (Carnier et al., 2000; Albera et al., 2001) but covariances between beef traits and calving performance are assumed to be null.

The aim of this study was to estimate genetic correlations between direct and maternal calving performance and beef traits for Piemontese cattle.

Material and Methods

Data

In the breeding program for the Piemontese breed sequential selection of sires is applied: young bulls are first selected on the basis of their own performance testing on station for beef traits and subsequently progeny tested for calving performance using birth records of their progeny and calving records of their daughters.

A total of 1,602 records of young bulls enrolled in the performance testing program from 1989 to 2002 at the central station of the Italian Piemontese Cattle Association were available.

At the station, bulls are weighed monthly from 2 up to 12 mo of age and daily gain (DG) is computed as the slope of the regression of live weight on age at weighing. For bulls tested after 1991 (1,292 bulls), scores for live fleshiness and bone thinness attributed by trained classifiers were also available. Fleshiness was appraised on six different body sites using a nine scores linear system: withers width (WW), shoulder muscularity (SM), limbs width (LW), limbs thickness (LT), thigh muscularity (rear view, TM), thigh profile (side view, TP). Bone thinness of the shin-bone (BT) was also evaluated with the same scale. Each animal was independently scored by three classifiers. Details on the performance testing procedure of Piemontese bulls can be found in Albera et al. (2001).

A recording system of calvings according to the level of difficulty was adopted in 1989. Five scores are used: 1 (unassisted delivery), 2 (assisted easy calving), 3 (difficult calving), 4 (Cesarean section), 5 (embryotomy). Information about presentations of calf was not systematically recorded, therefore it was impossible to exclude calving records with abnormal presentations. In order to estimate covariances between beef traits and calving performance, only informative calving records have been considered: birth records of tested bulls, of their sire and dam, half sibs, progeny and of the progeny of their half sibs. Furthermore, birth records of calves having a tested bull or its male half sib as maternal grandsire have been used. This editing had little impact on data structure for herds using artificial insemination as all the bulls selected for AI were also tested for beef traits on station. Since the use of AI is widespread in the Piemontese breed, analyzed records were around 70 % of the total records available. Discarded records were mainly from herds using natural service bulls, that were excluded from the analysis because of the lack of connectedness with young bulls tested for beef production traits.

Differences in the incidence of dystocia and in the magnitude of estimated genetic parameters suggested to treat calving performance in heifers and in cows as different traits (Carnier et al., 2000).

Incomplete records, records with missing sire, dam, maternal grandsire or granddam, records from twinning births or from very small herds (less then 30 records over 14 yr) have been removed.

After editing calving records and beef traits records were merged in order to form two datasets: dataset 1 included daily gain, live fleshiness traits, bone thinness of station tested bulls and calving records in the first parity, dataset 2 included the same information for beef traits associated with calving records in later parities. In dataset 2 cows included as dams were required to have at least two calving records as later parities.

Observations on daily gain, live fleshiness and bone thinness of calves not tested at station were treated as missing values. Similarly, for station tested bulls without their own birth record, observations on calving score were set to missing.

All available pedigree information (on average 4.5 generations of ancestors) was used to set up the numerator relationship matrix among animals.

After editing procedures datasets 1 and 2 contained 30,763 and 80,474 records, respectively, and the corresponding pedigree files 86,270 and 115,605 records.

Characteristics of the datasets are reported in Table 1.

Table 1. Number of records, animals, and herds in the two data sets

Item	Dataset 1	Dataset 2
Total records	30,763	80,474
Calving records	29,237	80,188
Beef traits records	1,602	1,602
Young bulls tested for beef traits		
with own birth record	76	1,316
with birth record of progeny	347	371
with calving records of daughters	260	201
Herds	467	471
Cows	29,237	21,496
Sires	1,831	1,871
Maternal grandsires	2,106	2,324
Sires being also maternal grandsires	1,157	897
Records in pedigree file	86,270	115,605

Models

A multivariate analysis including all the considered traits simultaneously was not feasible due to computing limitation. Therefore, covariance components have been estimated using bivariate linear animal models applied to calving performance (heifers or cows) and one beef trait at a time. For live fleshiness traits and bone thinness the average of the scores provided by the three classifiers was used.

The model used for the analysis of dataset 1 was

$$
\begin{bmatrix} \mathbf{y}^c \\ \mathbf{y}^b \end{bmatrix} = \begin{bmatrix} \mathbf{X}^c & 0 \\ 0 & \mathbf{X}^b \end{bmatrix} \begin{bmatrix} \mathbf{b}^c \\ \mathbf{b}^b \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_d^c & 0 & \mathbf{Z}_m^c \\ 0 & \mathbf{Z}_d^b & 0 \end{bmatrix} \begin{bmatrix} \mathbf{u}_d^c \\ \mathbf{u}_d^b \\ \mathbf{u}_m^c \end{bmatrix} + \begin{bmatrix} \mathbf{e}^c \\ \mathbf{e}^b \end{bmatrix}
$$

where $\mathbf{y}$ is a vector of observations, $\mathbf{b}$ is a vector of fixed effects, $\mathbf{u}_d$ is a vector of random additive genetic direct effects, $\mathbf{u}_m$ is a vector of random additive genetic maternal effects, $\mathbf{e}$ is a vector of random residual and $\mathbf{X}$, $\mathbf{Z}_d$ and $\mathbf{Z}_m$ are known incidence matrices relating observations to $\mathbf{b}$, $\mathbf{u}_d$ and $\mathbf{u}_m$. Superscripts denote observations and model terms related to

calving performance in the first parity (c) and the beef trait analyzed jointly (b). For random effects assumed means were null and variances were

$$
V \begin{bmatrix} \mathbf{u}_d^c \\ \mathbf{u}_d^b \\ \mathbf{u}_m^c \end{bmatrix} = \begin{bmatrix} \sigma_d^{2(c)} & \sigma_d^{(cb)} & \sigma_{dm}^{(c)} \\ \sigma_d^{(cb)} & \sigma_d^{2(b)} & \sigma_{dm}^{(cb)} \\ \sigma_{dm}^{(c)} & \sigma_{dm}^{(cb)} & \sigma_m^{2(c)} \end{bmatrix} \otimes \mathbf{A}
$$

$$
V \begin{bmatrix} \mathbf{e}^c \\ \mathbf{e}^b \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_e^{2(c)} & 0 \\ 0 & \mathbf{I}\sigma_e^{2(b)} \end{bmatrix}
$$

where σ_d^2 is the additive direct genetic variance, σ_m^2 is the additive maternal genetic variance, σ_d is the additive genetic covariance between direct effects, σ_{dm} is the additive

genetic covariance between direct and maternal effects, σ_e^2 is the random residual variance, $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{I}$ is an identity matrix and $\otimes$ is the Kronecker product operator.

Because a very low number of bulls tested on station were born from heifers (see Table 1) residual covariances between calving performance of heifers and beef traits have been assumed to be zero.

Dataset 2 was analyzed with a model similar to that used for dataset 1 but a permanent environmental random effect was included for calving performance

$$\begin{bmatrix} \mathbf{y^c} \\ \mathbf{y^b} \end{bmatrix} = \begin{bmatrix} \mathbf{X^c} & 0 \\ 0 & \mathbf{X^b} \end{bmatrix} \begin{bmatrix} \mathbf{b^c} \\ \mathbf{b^b} \end{bmatrix} + \begin{bmatrix} \mathbf{Z_d^c} & 0 & \mathbf{Z_m^c} & \mathbf{Z_p^c} \\ 0 & \mathbf{Z_d^b} & 0 & 0 \end{bmatrix} \begin{bmatrix} \mathbf{u_d^c} \\ \mathbf{u_d^b} \\ \mathbf{u_m^c} \\ \mathbf{u_p^c} \end{bmatrix} + \begin{bmatrix} \mathbf{e^c} \\ \mathbf{e^b} \end{bmatrix}$$

where $\mathbf{y}$, $\mathbf{b}$, $\mathbf{u_d}$, $\mathbf{u_m}$, $\mathbf{e}$, $\mathbf{X}$, $\mathbf{Z_d}$, $\mathbf{Z_m}$ have the same meaning as in the former model, $\mathbf{u_p}$ is a vector of random permanent environmental effects and $\mathbf{Z_p}$ is an incidence matrix relating observations on calving performance to their respective random permanent environmental effects. Superscripts indicate calving performance in later parities (c) and the beef trait (b). Random components of the model were assumed to have null means and variances as

$$\mathbf{V} \begin{bmatrix} \mathbf{u_d^c} \\ \mathbf{u_d^b} \\ \mathbf{u_m^c} \\ \mathbf{u_p^c} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_d^{2(c)} & \mathbf{A}\sigma_d^{(cb)} & \mathbf{A}\sigma_m^{(c)} & 0 \\ \mathbf{A}\sigma_d^{(cb)} & \mathbf{A}\sigma_d^{2(b)} & \mathbf{A}\sigma_{dm}^{(cb)} & 0 \\ \mathbf{A}\sigma_m^{(c)} & \mathbf{A}\sigma_{dm}^{(cb)} & \mathbf{A}\sigma_m^{2(c)} & 0 \\ 0 & 0 & 0 & \mathbf{I}\sigma_p^{2(c)} \end{bmatrix}$$

$$\mathbf{V} \begin{bmatrix} \mathbf{e^c} \\ \mathbf{e^b} \end{bmatrix} = \begin{bmatrix} \sigma_e^{2(c)} & \sigma_e^{(cb)} \\ \sigma_e^{(cb)} & \sigma_e^{2(b)} \end{bmatrix} \otimes \mathbf{I}$$

where $\sigma_{\mathbf{d}}^2$, $\sigma_{\mathbf{m}}^2$, $\sigma_{\mathbf{d}}$, $\sigma_{\mathbf{dm}}$, $\sigma_{\mathbf{e}}^2$, $\mathbf{A}$, $\mathbf{I}$ are defined as in the former model, $\sigma_{\mathbf{p}}^2$ is the random permanent environmental variance and σ_{e} is the random residual covariance. In this analysis residual covariance has been considered non-null because most of the bulls tested for beef traits also had their own birth record.

Heritabilities of calving performance were derived from estimated (co)variances as in Carnier et al. (2000). Correlations between additive direct or maternal additive genetic effects on calving performance and additive genetic effects on a beef trait have been computed as

$$\mathbf{r}_{\mathbf{d}}^{(\mathbf{cb})} = \frac{\sigma_{\mathbf{d}}^{(\mathbf{cb})}}{\sqrt{\sigma_{\mathbf{d}}^{2(\mathbf{c})} \sigma_{\mathbf{d}}^{2(\mathbf{b})}}} \quad \text{and} \quad \mathbf{r}_{\mathbf{dm}}^{(\mathbf{cb})} = \frac{\sigma_{\mathbf{dm}}^{(\mathbf{cb})}}{\sqrt{\sigma_{\mathbf{m}}^{2(\mathbf{c})} \sigma_{\mathbf{d}}^{2(\mathbf{b})}}}, \text{respectively.}$$

Nongenetic fixed effects

For calving performance in the first parity (dataset 1) vector of fixed effects included herd, year-season of calving, sex of the calf, age of the dam at calving and the interaction between sex of the calf and age of the dam. For calving performance of cows (dataset 2) effects of herd-year-season, age of the dam within parity and sex of the calf were considered. As the number of small herds was not trivial, the herd-year-season effect could not be considered in the model used for first parity; in the analysis of dataset 2 it was fitted only for large herds (herds with more than 200 calving records in 14 yr). For medium-sized herds (from 100 to 200 calving records) or small herds (less then 100 calving records) a herd-year or a herd effect were included, respectively. Two seasons of calving were defined, from November to April and from May to October. The age of the dam at calving was classified: eight classes (21 to 37 mo) for heifers and 50 classes within parity (seven parities) for cows.

For beef traits, fixed effects in the model were as in Albera et al. (2001). For DG and BT they included the contemporary group of animals on test (154 levels) and the parity of the dam treated in classes (four levels). For live fleshiness traits the linear regression effect of the weight of bulls at scoring on the fleshiness score was also fitted. As individual classifiers have changed over time it was impossible to include the effect of the classifier in the model adopted for the live fleshiness and bone thinness scores.

Because of missing genotype information for most animals, the effect of the genotype at the myostatin locus (Grobet et al., 1998) was not considered in the model both for calving performance and beef traits. However, genotyping of the Piemontese sires selected for artificial insemination in the last 30 yr revealed that all the bulls were homozygous for the mutated allele (A. Albera, unpublished data). Because the rate of AI is high in Piemontese cattle, the genotype at the myostatin locus cannot be considered as a source of variation for these traits.

All analyses were performed using average information REML (Gilmour et al., 2002).

Results and Discussion

Incidence of calving scores by parity is reported in Table 2. Heifers experienced more calving problems than adult cows; the amount of Cesarean sections was over three times higher for first than for later parities and also difficult calvings were two times more frequent in heifers than in cows. Despite the very low frequency of calving records scored as embryotomy, merging of these records with Cesarean sections was not considered because of the difference in the relative economic values (Albera et al., 1999).

Table 2. Incidence of calving scores by parity

	Parity	
Calving score	First, %	Second and later, %
1 Unassisted	14.1	23.4
2 Assisted easy	57.3	65.1
3 Difficult	13.7	7.8
4 Cesarean section	14.8	3.6
5 Embryotomy	0.1	0.1

Calving performance was analyzed with a linear model albeit threshold model methodology is the method of choice for the analysis of categorical traits (Gianola and Foulley, 1983). The use of a threshold model has been shown to lead to possible bias in the estimates of variance components (Moreno et al., 1997) when the number of progeny per sire is limited and one or more of the fixed effects included in the model have a large number of levels with a small number of observations within level. Furthermore, some problems in the estimation of fixed effects might also arise as a consequence of the extreme category problem, due to the occurrence of all observations for a class of a fixed effect in the same category of the response variable (Misztal et al., 1989). In such a situation, the use of linear models has been recently suggested as an acceptable solution to overcome data structure problems in the genetic evaluation of calving performance (Phocas and Laloë, 2003) and is currently adopted in the Piemontese breed (Carnier et al., 2000).

Heritabilities

Estimates of (co)variances, heritabilities and genetic correlations between direct and maternal genetic effects for calving performance in heifers and cows are presented in Table 3. Estimates obtained in different bivariate analyses were consistent and, for this, pooled estimates are presented. Variances and heritability estimates were similar to those obtained from Carnier et al. (2000) for Piemontese cattle.

Heritability for direct and maternal effects on calving performance was twice as high for heifers as for cows (0.16 and 0.11 vs. 0.07 and 0.06). Direct heritabilities were larger than heritabilities of maternal effects both in heifers and adult cows. In adult cows, variance due to permanent environmental effect was lower than direct and maternal variances.

Estimated heritabilities were slightly lower for direct effects or slightly higher for maternal effects than those reported by Carnier et al. (2000). Genetic covariances between direct and maternal effects were negative; as a consequence, the corresponding genetic correlations were also negative, -0.38 and -0.33 in the first and later parities respectively, but their magnitude was smaller in comparison with estimates of Carnier et al. (2000). Although a sample of all available calving records has been used, results indicate that the sampled data represented the complete population well.

Table 3. Estimated (co)variances and heritabilities for calving performance scores

Parameter[a,b]	Parity	
	First	Second and later
σ^2_d	0.108	0.028
σ^2_m	0.077	0.024
σ_{dm}	-0.035	-0.009
σ^2_p	-	0.019
σ^2_e	0.531	0.322
$h^{2\,c}_d$	0.158	0.074
$h^{2\,c}_m$	0.114	0.064
$r_{dm}^{\ d}$	-0.380	-0.333

[a]*Subscripts d, m, p and e indicate respectively direct additive genetic, maternal additive genetic, permanent environmental and residual effects.*
[b]*Estimated parameters from pooled bivariate analyses with beef production traits.*
[c]*Standard errors of heritabilities ranged from 0.008 to 0.024.*
[d]*Standard errors of genetic correlations were 0.088*

Differences with Carnier et al. (2000) can be ascribed to the use of different models: in this study a multiple trait model has been used and effects due to selection on beef traits occurring in an earlier stage are accounted for.

The effect of selection on the first calving performance on estimated genetic parameters for calving performance in subsequent parities could not be considered.

Estimated variances and heritabilities for beef traits are reported in Table 4.

Estimated parameters for beef traits obtained in bivariate analyses with calving performance of heifers were consistent with those from analyses with calving performance of cows. In agreement with results by Albera et al. (2001), daily gain was the beef trait with the highest estimated heritability. Live fleshiness and bone thinness were moderately heritable traits with estimates ranging from 0.29 to 0.47.

In comparison with the current study, Albera et al. (2001) reported higher heritabilities for WW, SM and LW and lower estimates for TM and TP. These differences might be related to the use of bivariate models considering also calving performance. It should also be noted that the amount of information on beef traits available for this study was almost doubled. This is not expected to affect the estimates of genetic parameters but only the magnitude of standard errors.

For live fleshiness, that was subjectively scored by classifiers who changed over time, estimates might also differ due to the inclusion of new data, even though preliminary analyses showed a limited heterogeneity of variance across classifiers. The same change could not be observed for DG probably because of the objective nature of weight data.

Table 4. Estimated variances and heritabilities for beef traits

Trait	Parameter[a,b]		
	σ_d^2	σ_e^2	$h_d^{2\ \text{c}}$
Daily gain, kg/d	0.007	0.005	0.591
Withers width, points	0.246	0.450	0.354
Shoulder muscularity, points	0.220	0.450	0.329
Loins width, points	0.145	0.345	0.296
Loins thickness, points	0.143	0.345	0.293
Thigh muscularity, points	0.441	0.492	0.473
Thigh profile, points	0.353	0.496	0.416
Bone thinness, points	0.222	0.322	0.409

[a]*Subscripts d and e indicate respectively direct additive genetic and residual effects.*
[b]*Estimated parameters from pooled bivariate analyses with calving performance score.*
[c]*Standard errors of heritabilities ranged from 0.076 to 0.086.*

Correlations between calving performance and beef traits

Estimates of genetic covariances and correlations between beef traits and direct or maternal calving performance for first and later parities are presented in Tables 5 and 6, respectively.

Table 5. Estimates of direct and maternal genetic covariances and correlations between calving performance scores in the first parity and beef traits

Beef traits[b]	Parameter[a]			
	σ_d	σ_m	r_d [c]	r_m [d]
Daily gain	0.012	-0.005	0.425	-0.232
Withers width	-0.011	0.043	-0.065	0.312
Shoulder muscularity	0.012	0.035	0.076	0.264
Loins width	0.022	0.019	0.183	0.183
Loins thickness	0.011	0.006	0.089	0.056
Thigh muscularity	0.045	0.047	0.211	0.259
Thigh profile	0.021	0.053	0.110	0.330
Bone thinness	-0.026	0.039	-0.172	0.314

[a]*The term σ_d is the genetic covariance between direct additive genetic effects of calving performance score and the beef trait, the term σ_m is the genetic covariance between maternal additive genetic effect of calving performance score and additive genetic effect of the beef trait, the term r_d is the genetic correlation between direct additive genetic effects of calving performance score and the beef trait, and r_m is the genetic correlation between maternal additive genetic effect of calving performance score and additive genetic effect of the beef trait.*
[b]*Estimated parameters from separate bivariate analyses with calving performance score. Units of measurement: Daily gain, kg/d; Withers width, Shoulder muscularity, Loins width, Loins thickness, Thigh muscularity, Thigh profile, Bone thinness, points.*
[c]*Standard errors of genetic correlations between direct effect of calving performance score and beef traits ranged from 0.10 to 0.17.*
[d]*Standard errors of genetic correlations between maternal effect of calving performance score and direct effects of beef traits ranged from 0.11 to 0.16.*

Standard errors of genetic correlations were relatively high due to the particular structure of the data. As a consequence of the limited number of animals having phenotypic information on both calving performance and beef traits, covariances have been essentially

estimated through pedigree information. Furthermore, traits were measured in different environments as beef traits were recorded on central station whereas calving performance records were collected in the farms. The magnitude of standard errors in this study was in the range of literature reports for genetic correlations estimated between traits measured on bulls during performance testing in central station and traits measured on their progeny using field data (Oikawa et al., 2000; Eriksson et al., 2002).

Table 6. Estimates of direct and maternal genetic covariances and correlations between calving performance scores in second and later parities and beef traits

Beef traits[b]	Parameter[a]					
	σ_d	σ_m	σ_e	r_d [c]	r_m [d]	r_e
Daily gain	0.007	-0.004	0.001	0.499	-0.279	0.011
Withers width	-0.010	0.020	0.013	-0.126	0.257	0.034
Shoulder muscularity	0.001	0.013	0.010	0.006	0.179	0.026
Loins width	-0.008	0.018	0.010	-0.126	0.300	0.029
Loins thickness	-0.008	0.012	0.012	-0.130	0.205	0.035
Thigh muscularity	0.008	0.024	0.021	0.069	0.231	0.053
Thigh profile	0.016	0.017	0.009	0.158	0.179	0.024
Bone thinness	-0.030	0.029	-0.010	-0.379	0.396	-0.030

[a]*The term σ_d is the genetic covariance between direct additive genetic effects of calving performance score and the beef trait, the term σ_m is the genetic covariance between maternal additive genetic effect of calving performance score and additive genetic effect of the beef trait, the term σ_e is the residual covariance between calving performance score and the beef trait, the term r_m is the genetic correlation between direct additive genetic effects of calving performance score and the beef trait, r_m is the genetic correlation between maternal additive genetic effect of calving performance score and additive genetic effect of the beef trait, and r_e is the residual correlation between calving performance score and the beef trait.*

[b]*Estimated parameters from separate bivariate analyses with calving performance score.Units of measurement: Daily gain, kg/d; Withers width, Shoulder muscularity, Loins width, Loins thickness,Thigh muscularity, Thigh profile, Bone thinness, points.*

[c]*Standard errors of genetic correlations between direct effect of calving performance score and beef traits ranged from 0.08 to 0.14.*

[d]*Standard errors of genetic correlations between maternal effect of calving performance score and beef traits ranged from 0.10 to 0.15.*

Daily gain showed a positive genetic relationship with direct calving performance. Genetic correlations ranged from 0.42 in heifers to 0.50 in cows, providing evidence that animals having faster growth are likely to generate progeny experiencing more problems at birth. Since birth weight is known as the most important factor affecting the birth ability of calves (Meijering, 1984), the genetic correlation between DG and direct calving performance indicates that genes controlling growth before birth are also partly involved in the expression of post-natal growth.

Few studies dealt with the relationship between calving performance and traits related to beef production. In a literature survey, Koots et al. (1994) reported an average genetic correlation between post-weaning growth and direct calving ease similar to that of this study. Bennett and Gregory (2001) in a study involving several parental beef breeds and composite populations found a genetic correlation of 0.36 between post-weaning gain and direct calving difficulty score across breeds. Lower correlations have been reported by Gregory et al. (1995).

Maternal calving performance was negatively associated with DG both in first and later parities. Hence, calving ability is improved in females having higher growth rate. A possible biological explanation of this association might be related to the positive correlation between growth rate and mature weight of dams (Koots et al., 1994), which results also in a larger pelvic inlet of cows and in a better aptitude to calve. However, evidence of associations between calving ability of cows and their body weight or size is not reported in the literature. On the basis of the magnitude of the estimated genetic correlations, selection for enhanced growth rate of animals is expected to affect more intensively direct than maternal calving performance, causing an increase in the incidence of dystocia as a correlated response. The same pattern has been found by Averdunk et al. (1987) and Bennett and Gregory (2001) who reported genetic correlations of growth with calving ease stronger for direct effect than for maternal effect.

Genetic correlations between direct calving performance and live fleshiness traits were low to moderate. In the first parity all correlations were positive with the exception of that with WW, suggesting that as far as the muscularity of animals increases due to selection births become slightly more difficult. Among fleshiness traits, those related to the development of animals in terms of width, LW and TM, showed the higher correlations with direct calving performance. In later parities evidence of association between live fleshiness and birth ability of calves was not clear because some of the correlations were slightly

negative and in general their size was lower compared to first parity. Since the dimension of pelvic area of cows increases with age, it might be possible that calf conformation and shape do not act as a limiting factor in the calving process of adult cows. Similar results have been reported by Gregory et al. (1995) in beef cattle, who found a genetic correlation of 0.33 between muscle score of young bulls born from 2-yr old dams and their calving difficulty score. When considering young bulls born from more mature cows (over 3-yr old) the genetic correlation was lower and negative.

Other literature reports indicated inconsistent (Renand, 1985) or small positive association (Averdunk et al, 1987) between direct calving difficulties and traits expressing muscular development of young bulls.

Maternal calving performance showed a moderate positive association with all live fleshiness traits. Genetic correlations ranged from 0.06 to 0.33 in the first parity and from 0.18 to 0.30 in subsequent parities. Selection for increased muscularity is therefore likely to have a detrimental effect on the calving ability of females, probably due to a reduction in the pelvic inlet dimension. Phenotypic relationship between cows' muscularity and pelvic area has not been demonstrated in normally muscled breeds (Meijering, 1984), but has been reported for double muscled cattle (Hanset and Jandrian, 1979). The only study that could be found in literature concerning genetic correlation between live muscularity of bulls and maternal calving performance of their daughters indicated a lack of relationship between these traits (Averdunk et al., 1987). Unlike daily gain, live fleshiness traits were more correlated with calving performance as a trait of the dam than as a trait of the calf.

Bone thinness was negatively correlated with direct calving performance. Animals with thick bones are born with relatively more calving problems. Genetic correlation was larger for later parities compared to the first parity (-0.38 vs. -0.17). Genetic correlations of maternal calving performance with bone thinness were positive both for heifers and cows. Because skeletal development is related to size and weight, animals with thin bones probably also tend to be lighter at birth and this could explain the favourable correlation with direct calving performance. For the same reason calving ability of females is expected to be poorer in thin-boned cows because of the reduced body development. Furthermore, a positive association has been reported between bone thinness and live fleshiness in Piemontese (Albera et al., 2001) which might affect the dimension of dams pelvic area. Renand (1985) in French beef breeds, using data from two different progeny testing station,

reported inconsistent genetic correlations between skeletal development of young bulls and their birth difficulty ranging from positive to moderately negative depending on the station.

Residual correlations of calving performance in second and later parities with all of the beef traits were close to zero as expected since the traits were measured in different environments and only few animals had observations in both traits.

Implications

This study provides evidence of a genetic relationship between calving performance and traits related to beef production. Most of the estimated correlations are biologically unfavourable to the simultaneous improvement of calving performance and beef traits through selection. A complicating factor is due to direct and maternal effects of calving performance that often show genetic correlations of opposite sign with beef traits. The estimated genetic correlations will be used for the definition of a selection criterion including both calving performance and beef production traits. Appropriate selection strategies need to be implemented in order to improve the investigated traits.

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Chapter 6

General discussion

Introduction

In Chapter 1 the importance of calving performance in cattle population was outlined both from an economic and social perspective. It was concluded that in particular in cattle breeds highly specialized for beef production, breeding programmes should incorporate calving performance.

In the Piemontese breed, after over 15 yr of selection for beef production traits, it was decided to consider also calving performance as a trait in selection. Therefore, a new breeding goal has been set up and economic values have been estimated for all traits (Chapter 2).

Development of methods to predict breeding values for calving performance was the subsequent step to be accomplished. Genetic parameters needed to perform genetic evaluations have been provided for calving performance (Chapter 3) and beef traits (Chapter 4). Calving performance showed enough genetic variation to be improved through selection. However, estimation of genetic correlations between calving performance and beef production traits revealed conflicting relationships that limit the possibility of simultaneous improvement of all traits (Chapter 5). Moreover, direct and maternal components of calving performance showed genetic correlations of opposite signs with beef traits, complicating the establishment of a selection procedure. As a consequence, particular attention must be paid to including calving performance in the design of the breeding programme. Different alternatives need to be studied in order to define a proper strategy.
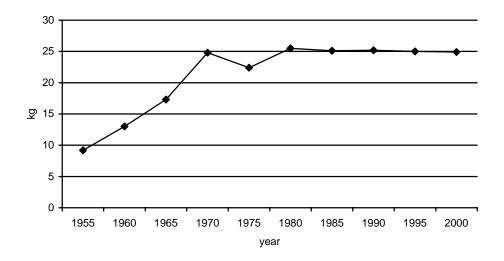
This chapter aims at the definition of a selection index and at the evaluation of the obtainable response to selection using different indices and breeding schemes. Issues concerning development and perspectives for the Piemontese breed are discussed.

The Piemontese breed

The Italian beef market and the position of the Piemontese

In Italy, beef consumption increased widely up to the Seventies as a consequence of the improved economic conditions of the population (Graph 1). During the Eighties consumption was steady, as a consequence of relative lower price of poultry and pork meat. The tendency in the Nineties was similar, reflecting consumer concerns about the possible negative effect of products of animal origin on human health, essentially due to fat content. The occurrence of B.S.E. disease affected the consumption, showing a strong reduction in 2001 (-11%) only partly recovered in subsequent years (Ismea-Osservatorio Latte, 2004).

Since the Fifties, the national production was not able to satisfy the increasing demand for beef. This led to import beef or live animals to be slaughtered but also young calves of beef breeds, to be fattened in specialised farms. Starting from the Eighties, the national production stabilised between 800 and 900 thousands tonn/yr equivalent to 60 to 65% of beef consumption (Ismea, 2004).

Graph 1. Per capita consumption of beef in Italy

The major interest in the Italian beef market is for lean meat: over 70% of the dead weight from slaughtering comes from young bulls that largely belong to specialised beef breeds. The slaughter of cows accounts for around 15% of total dead weight and the remaining comes from veal production by male calves of dairy herds (Ismea, 2004).

The population of suckler cows in Italy consists of 430,000 cows (18% of the total cows) belonging, to a large extent, to the Italian beef breeds (Ismea, 2004). Each of these breeds has a specific regional distribution, related to its area of origin. The Piemontese is located in the North-Western part of the country and is numerically the most important among the Italian breeds representing over 30% of the suckler cows bred in Italy. The population of Piemontese showed a strong decline in the last 40 yr, from 650,000 to 320,000 heads, due to the structural changes of the agricultural sector inducted both by the national and Europeran policies. These policies aimed to reduce the relative number of small farms to increase the average farm profitability. In the Piemonte region, between 1960 and 2000, the total number of cattle dropped from 1 milion to 800,000 heads and the number of farms showed a 90% reduction with a consistent increase in their size (Soster, 2005). Furthermore, the increasing specialisation of the Northern areas of Italy for milk production, fostered the introduction of high production dairy breeds, like Holstein Fresian, at the expense of local beef breeds.

Currently, the cattle production system of the Piemonte region is splitted into three systems, each system having the same numeric importance: Piemontese cattle, dairy cattle and imported calves to be fattened (Direzione Sanità Pubblica.- Regione Piemonte, 2003).

The contribution of each Italian breed to the national beef production is moderate, but their importance for the local regional market is consistent. Albera (unpublished data) estimated that the beef produced by Piemontese cattle was around 5% of the total beef produced in Italy, but represented almost 40% of that produced in the Piemonte region.

The market of the Piemontese beef has always been mainly local, based on traditional butcher shops and on individual trade of animals. More recently, also some chains of large-scale retail trade started to sell Piemontese beef, extending the market even outside its typical area of consumption. This new form of distribution, accounts for around 25% of the Piemontese beef market now (Albera, unpublished data).

The quality attributes of Piemontese beef, especially in terms of leanness, are appreciated on the local market and justify the higher price paid for the animals of this

breed. Compared to Blonde d'Aquitaine, Limousine and Charolais, which are the majority of foreign breeds whose calves are fattened in Italy, the market price of Piemontese young bulls is 6, 16 and 22% higher, respectively (Camera di Commercio di Cuneo, 2005).

Characteristics of the Piemontese breed

The main feature of the Piemontese breed is double muscling, due to a mutation in the myostatin coding sequence (Grobet et al., 1998). This characteristic was reported for the first time in 1886 (Raimondi, 1962). In the first part of the 20th century the practice of breeding double muscled animals was discouraged by the selection organisations, due to viability problems and abnormalities in the calves. However, the benefits in terms of growth, feed efficiency, dressing percentage and carcass composition played a major role in the farmers choices and contributed to the success of double muscled animals (Raimondi, 1962).

Bonadonna (1959) reported that 65% of the Piemontese bulls used for reproduction were phenotypically of double muscle type. The proportion of double muscled females used for breeding was much lower: farmers tended to use these females especially for fattening due their lower reproduction efficiency resulting from fertility and dystocia problems. However, the dispersion process of the myostatin mutated allele, driven by the economic advantages of double muscled animals and by the spread of AI, continued rapidly.

The mutated allele is now proximate to fixation in the Piemontese population. Testing of all AI sires selected in the last 30 yr revealed only homozygous animals. In a sample of 996 breeding females randomly choosen, only 4% of the animals were heterozygous at the myostatin locus, the others being homozygous with respect to the mutation (Anaborapi, 2004).

Evidence of good attributes of Piemontese animals both for quantitative and qualitative aspects of beef production has been provided by the studies of Tartari et al. (1988), Destefanis (1988) and Destefanis et al. (1988). These researches, comparing different breeds, showed the superiority of Piemontese young bulls in dressing percentage, retail products and eating quality. The meat of Piemontese was more tender even though its fat content was lower. However, the same studies also indicated that the growth performance of Piemontese animals was poorer than that of other specialised beef breeds.

In crossbreeding, favourable effects inducted by using Piemontese terminal sires have been reported on dressing percentage, carcass weight, lean meat production and tenderness

in dairy (Bonsembiante et al., 1975; Gigli et al., 1987) and beef cattle (Tatum et al., 1990; Wheeler et al., 1996; Wheeler et al., 1997).

Production system

The production system of Piemontese cattle is based on family farms of medium size. The transformation process of the Italian agricultural system affected also the structure of Piemontese cattle farms. During the last 40 yr a reduction in the number of farms was observed together with a consistent increase in farm size. The very small farms were unable to face market challenge and disappeared, whereas larger farms tended to increase the number of animals to become more competitive. The number of cows per herd in the registered farms increased from 12 to 28 in the last 30 yr (Anaborapi, 1988; Anaborapi, 2004).

Typically, the Piemontese suckler cows breeding and young bulls fattening are integrated in the same farm. This production system is practiced in over 75% of the farms (Bona et al., 2005). Only a limited number of calves are fattened in specialised fattening farms.

The traditional breeding system is tightly linked to the usage of farm land: 90% of feeds used for animals are produced in the farm itself and usually only the protein supply is purchased from the market (Bona et al., 2005). Most of the Piemontese farms are located in the flat area of the Po river where the cost of land is high. As a consequence, the surface of the farms is usually limited leading to a semi-intensive form of husbandry, with an average animal intensity around 2.8 livestock units per hectare (Bona et al., 2005). For the same reason grazing is practiced only in 25% of the farms, even though grassland covers over 40% of farm land (Bona et al., 2005).

The transformation in the structure of the breeding programme

The systematically organized genetic improvement of the Piemontese is quite recent. The herdbook was founded in 1960. The main concern was to breed animals consistent with the defined breed standard following the so-called "ideal type".

At the beginning of the Seventies a progeny testing programme was set up, aimed to improve beef production and calf characteristics (Maletto, 1971). However, appearance was still predominant in selection decisions. Selection candidates were chosen based on their phenotype for beef traits among the sires already used for natural service or at shows. The
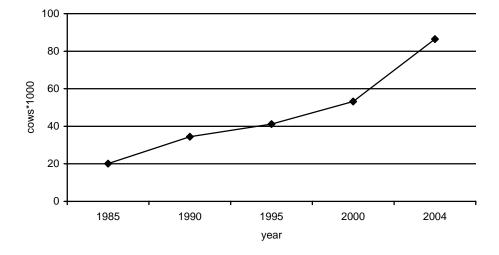
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choice was made by a commission including breed experts, technicians and farmers. After progeny testing, bulls showing best results were selected for AI, again using only phenotypic information on progeny. Genetic evaluations were not performed and a selection criterion was not clearly defined. A group of elite breeders provided most of the bulls for testing and also a consistent number of breeding stock for other farmers. These breeders were the farmers with registered animals. The typical pyramidal structure of animal breeding industry was already represented even though the definition of genetically superior animals was not objective.

In 1985 selection of Piemontese came to a turning point: a genetic station for performance testing was established to measure beef production traits on selection candidates under uniform conditions. Genetic evaluations, initially based on the adjustments of phenotypic performance for non-genetic factors, eventually incorporated pedigree information and BLUP methodology to improve the accuracy of predictions. A breeding programme was implemented and a selection criterion including growth and live fleshiness was developed. In 1989 the systematic recording of calving scores and calf characteristics in the farms was started to provide information for the improvement of calving performance.

A further boost to the application of the breeding programme was given by the use of AI, which moved from 20% in the beginning of the Eighties to over 60% in 1995 (Anaborapi, 1995). This percentage, high for a beef breed, was made possible by the semi-intensive production system of Piemontese cattle and by the medium size of farms.

The number of registered cows (Graph 2) showed a spectacular increase in the last 20 yr   (Anaborapi, 1985; Anaborapi, 2004) due to an increase in registration rate. In the same period the incidence of registered cows on the total Piemontese cows population raised from 8 to 61%. The reasons of this increase are related to the technical and information support available to registered herds and to the economic advantages in obtaining governmental subsidies. In the last 5 yr registration in the herdbook also allowed farmers to obtain higher prices for slaughter animals due to the breed certification of their animals, which is recognised by the market.

A high number of new herds became available to contribute to the breeding programme that was in development since 1985. The use of objective and scientific methods in genetic evaluations shifted the perspective of selection from type to productivity. The relatively large use of AI and the active involvement in the programme, through the use of young bulls and more recently through contact matings, allowed also the new farmers to

supply bulls for testing. This caused a re-definition of the elite breeders: at the top of the pyramid there were no longer few breeders with animals of outstanding performance on the shows, but a wide group of herds with genetically superior animals in the selected traits.

Graph 2. Cows registered in the Piemontese herdbook

In most cases, the old elite breeders criticized the results obtained with the application of the programme, claiming that type traits, being not considered, were worsening and this would have led to a loss of the original breed characteristics. They rarely contributed to the programme and moved their activity mainly to the shows, enforcing their arguments about the importance of appearance. They faced the competition with the new breeders for social status but also with the expansion in the use of AI, that was reducing their market for natural service bulls. However, still holding relevant positions within breeders organisations, they were able to exert some influence on decision making, sometimes slowing the selection process.

As results of genetic improvement for beef traits were soon evident, the transformation process in the nucleus of selection was completed in a few years. The use of predicted breeding values by the farmers is now widespread and some of the former elite breeders are trying to recover their position within the breeding programme, accepting the new selection methods.

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In recent years, the main interest in the development of the breeding programme was the introduction of calving performance among the selected traits. The association between muscular hypertrophy and calving problems is well known (Menissier, 1982). However the study of Carnier et al. (2000) showed that additive genetic variation for direct and maternal calving performance exists in the Piemontese population, even though the myostatin mutated allele *mh* is almost fixed (Anaborapi, 2004).

The incidence of calving difficulties in the Piemontese breed is consistent but not extreme as in other double muscled breeds: cesarean section are practiced in 13% of the first calvings but reduce to 4% in later parities, unassisted or easy assisted calvings sum up to 70 and 85% in heifers and cows, respectively (Carnier et al., 1998). These results could be related to the selection decisions of breeding females made by farmers in the past, excluding heavy muscled heifers from reproduction (Bonadonna, 1959).

Since 2000 genetic evaluations for direct and maternal calving performance in first and later parities are routinely performed using the estimates of genetic parameters obtained from the research conducted within this thesis. A selection index including beef traits and calving performance has been established in the same year. Currently, traits are assumed to be genetically independent and are weighted according to empirical weights in the index.

Development of the breeding programme

In this section the design of the breeding programme to select beef production traits and calving performance is addressed. As a first step, cumulative discounted expressions are computed and used, together with economic values, to weight the traits in the breeding goal. Subsequently, the response of several breeding programmes is simulated in order to identify the most appropriate selection strategy. Simulated breeding programmes differ in design parameters such as intensity of selection and accuracy of predicted breeding values, reflecting the use of different sources of information. The effect of using alternative sets of economic values is also evaluated.

Cumulative discounted expressions

Selection index theory requires that additive genetic values of traits in the aggregate genotype are weighted by their economic values, which express the marginal return per unit of improvement in each trait (Hazel, 1943). Often the traits in the breeding goal differ in degree and timing of expression of genetic superiority originating from selected animals. These unequal expressions need to be accounted for in the breeding goal. The geneflow method (Hill, 1974) allows to follow the process of dissemination of superior genes in the population and to compute cumulative expressions of genes over time. Cumulative expressions are then discounted to the net present value in order to consider different times of expression.

In the breeding goal of Piemontese cattle (Albera et al., 2004a) traits are unequally expressed: beef traits are expressed by slaughter animals, direct calving performance by newborn calves and maternal calving performance by breeding females. Therefore, cumulative discounted expressions for these traits have been computed using the Gflow computer program (Brascamp, 1978).

Cumulative discounted expression c_{lt} is derived as

$$c_{lt} = \sum_{i=0}^{t} \mathbf{h'm}_{li}\delta^{i}$$

where t is time horizon, l is selection path, $\mathbf{h}$ is the incidence vector that specifies the contribution of age-classes to phenotypic expression of traits, $\mathbf{m}_{li}$ specifies the relative contribution of the initial set of genes in the selected animals (through selection path l) to

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the genes of animals in this age-class at time i, and δ^i is the factor that discounts future revenues to the present year. The number of rows in **h** and **m** equals the number of age-classes over tiers and sexes within the considered tiers.

Cumulative discounted expressions differ between selection paths; selected individuals are sires to breed sires, sires to breed dams, dams to breed sires and dams to breed dams (path SS, SD, DS and DD, respectively). In the calculation of $\mathbf{m}_{li}$ two matrices, **R** and **Q**, describing the flow of genes through the population by reproduction and aging, respectively are used (Brascamp, 1978). The **P** matrix resulting from **R** + **Q** defines the transmission of genes from parents to offsprings in the population.

In this study a nucleus with eight male and eight female age-classes and a commercial tier with two age-classes for slaughter animals without sex distinction have been considered. Length of age-classes was one year. The corresponding **P** matrix was

$$
\mathbf{P} = \begin{bmatrix} \mathbf{P_{SS}} & \mathbf{P_{DS}} & 0 \\ \mathbf{P_{SD}} & \mathbf{P_{DD}} & 0 \\ \mathbf{P_{SC}} & \mathbf{P_{DC}} & 0 \end{bmatrix}
$$

where P_{SS}, P_{SD}, P_{DS} and P_{DD} are submatrices describing gene transfer by selection path and P_{SC} and P_{DC} are submatrices describing the flow from the nucleus to the commercial tier.

Definition of matrices was according to the structure of the Piemontese herdbook population, assuming a breeding programme based on progeny testing of AI bulls for direct and maternal calving performance.

The incidence vectors **h** were defined according to production and reproduction levels and replacements times. The beef traits (BT), daily gain and live fleshiness, were expressed by commercial animals slaughtered at 16 mo of age (age-class 18). Since relative incidence of males and females for slaughter was already considered in the estimation of economic values for beef traits (Albera et al., 2004a), incidence vector for BT contained only a nonzero element, 1, for two years old commercial animals. Among calving traits, direct calving performance in cows (CP_d) and maternal calving performance in heifers (CP_m) were considered in this study. As the assumed rate of AI was 100%, only few males were needed for reproduction. Therefore, expression of CP_d was considered only for newborn commercial animals (age-class 17) and females in the nucleus (age-class 9) and not for male

calves in the nucleus. Maternal calving performance was expressed by females in age-class 11, calving at the age of 28 mo.

As in all traits expression of genes was not exactly at the end of the age-class, additional time adjustments were introduced within age-classes discounting revenue from the last day of the age-class to the average moment of expression.

In the study a time horizon of 20 yr, defining the period of evaluation of future genes expressions by offspring of an initial set of selected individuals, was considered. The discounting factor δ was computed according to Smith (1978)

$$\delta^i = \left(\frac{1}{1+q}\right)^i$$

where *q* is the inflation free interest rate. The value of *q* in this study was set at 0.03, corresponding to the average value for the period 1998-2002 in Italy (Statistical Office of the European Communities, 2004).

For each trait the cumulative discounted expression was computed as the sum of the cumulative discounted expressions obtained for the three sire paths: sires to breed sires (SS), sires to breed dams (SD) and sires to breed commercial slaughter animals (SC). Obtained cumulative discounted expressions for the traits in the breeding goal of Piemontese cattle are reported in Table 1.

Table 1. Cumulative discounted expressions of traits per selection path

Traits[b]	Selection path[a]			
	SS	SD	SC	Sum
BT	0.320	0.323	0.404	1.047
CP_d	0.362	0.411	0.381	1.154
CP_m	0.283	0.668	0.000	0.951

[a]*SS = sires to breed sires; SD = sires to breed dams; SC = sires to breed commercial slaughter animals.*

[b]*BT = beef traits (daily gain, live fleshiness); CP_d = direct calving performance; CP_m = maternal calving performance.*

The observed differences between traits and selection paths originate from the relative incidence in genes expression and on the time lag between the moment of genes introduction and that of their expression in the population. Gene flow method tends to increase the relative importance ot traits expressed early in the life of animals. For this reason CP_d, that is expressed at birth, showed the highest values followed by BT, which are expressed in the second year of life by slaughter animals. The impact of CP_m was proportionally reduced because this trait is expressed only by females and later in life compared to the other traits.

Among selection paths, SC showed high values for BT and CP_d and zero values to CP_m; this path involves a large share of the animals in the population, but limited only to traits expressed in the production population. Cumulative discounted expressions for maternal calving performance were higher in the SD compared to the SS path because this trait was directely expressed by the female progeny of sires, whereas SS contributed to female traits via their sons only. The lack of expression of direct calving performance in the male calves explains the lower values obtained in the SS path for this trait.

Evaluation of selection strategies

Estimated genetic parameters (Carnier et al., 2000; Albera et al., 2001; Albera et al., 2004b) and discounted economic values, resulting from the multiplication of economic values (Albera et al., 2004a) times cumulative discounted expressions, have been used to evaluate the response to selection.

The traits considered in the breeding goal and in the index were daily gain (DG), live fleshiness (Flesh), direct calving performance in cows (CP_d) and maternal calving performance in heifers (CP_m). Among several fleshiness traits measured on Piemontese young bulls (Albera et al., 2001), thigh muscularity has been chosen to represent Flesh. The choice to include direct calving performance in cows and maternal calving performance in heifers as calving traits is related to the availability of information for breeding values prediction of selection candidates: progeny tested bulls are preferentially mated to adult cows and their first evaluation for maternal calving performance is based on the calving of their daughters as heifers. Direct calving performance in heifers and maternal calving performance in cows have not been included considered because of the lag in obtaining information and due to the very high genetic correlations with CP_d and CP_m, respectively (Albera et al., 2004b).

Several selection stategies have been compared in terms of response to selection. Alternative breeding programmes have been evaluated with deterministic simulations, considering discrete generations and truncation selection (Rutten et al., 2002). Multistage selection schemes have been simulated in order to represent the situation of the Piemontese breed, where bulls to be progeny tested are selected after their own performance testing on station for beef traits.

The simulated breeding programmes differed in the traits considered and in the selection methods: in breeding programme 1 selection was for beef traits only; the breeding goal of programme 2 included also CP_d; in programme 3 CP_m was added to the traits measured in programme 2; specialised sire and dam lines, selected for beef and maternal traits respectively, were considered in programme 4.

In the definition of the breeding goal of programmes 1, 2 and 3 traits were progressively included in order to provide an overall evaluation of the costs and benefits, in terms of response to selection, due to introduction of calving performance in the breeding goal. The loss in beef traits resulting from the selection for calving traits could be quantified. In the same way, the effect of selection for beef traits only, could be estimated by calculating the correlated response obtained for calving performance in breeding programme 1. Finally, comparison between programmes 2, 3 and 4 allows the identification of the most appropriate selection strategy.

Genetic, phenotypic and economic parameters of the traits considered in the simulated breeding programmes are summarized in Table 2.

Characteristics of the simulated breeding programmes

In all programmes 20 bulls and 10,000 cows per generation were selected, corresponding to a selection proportion of 0.005 and 0.5, respectively. The number of bulls station-tested was fixed to 216 which is the current testing capacity of Piemontese genetic station.

Beside the base situation, several options have been studied within each programme. The relative economic values of traits have been modified in order to obtain the desired response in individual traits. Consequences of changes in the accuracies of predicted breeding values for calving traits, obtained by increasing the number of progeny of bulls on test, have been investigated. Finally, the effect of changes in the generation interval has also been appraised, comparing progeny testing schemes having different length. In order to be

able to compare programmes differing in the generation interval, response to selection per year was calculated.

Table 2. Genetic, phenotypic and economic parameters for the traits considered in the breeding programme. Heritabilities (diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal)

Traits[a]	DG	Flesh	CP$_d$	CP$_m$	σ$_G$[b]	Discounted economic value[c]
DG, g/d	0.60	-0.25	0.50	-0.23	77.46	0.21
Flesh, points	0.07	0.45	0.07	0.26	0.63	59.69
CP$_d$, points	0.11	0.05	0.08	-0.50	0.17	-90.25
CP$_m$, points	-0.05	0.06	0.04	0.09	0.25	-23.72

[a]*DG = daily gain; Flesh = live fleshiness; CP$_d$ = direct calving performance; CP$_m$ = maternal calving performance.*
[b]*Genetic standard deviation.*
[c]*€*year^{-1}*cow^{-1}*trait unit^{-1}.*

Breeding programme 1 – selection for beef traits only

In this programme only beef production traits were selected using information provided by performance testing of young bulls on station. Two-stage selection was practiced: the first stage corresponded to pre-selection of male candidates to be station-tested based on pedigree information, the second stage was selection at the end of performance testing. Selected proportion of sires was 0.05 in first stage and 0.09 in second stage. Females were selected in the second stage. In the last stage, the selection of bulls was based on an index including their own performance and the performance of 10 half-sibs. Selection index of females was based on the information provided by their male half-sibs station-tested. Assumed generation interval was 26 mo for sire to sire and 38 mo for dam to sire paths.

Breeding programme 2 – selection for beef traits and direct calving performance

This programme was similar to programme 1 but a third stage of selection was introduced: after performance testing, selected bulls were progeny tested for CP$_d$ up to the birth of their progeny. In second stage, 40 bulls were selected (selection proportion 0.19)

and half of them were finally selected after progeny test. All females were selected after third stage. Index information of selection candidates for CP_d was based on their own and 99 half-sibs performance in first and second stages. In third stage, 100 progeny were produced for each bull. For beef traits information were as in programme 1. Assumed generation interval was 36 mo for sires to sire and 38 mo for dams to sire.

Breeding programme 3 – selection for beef traits, direct and maternal calving performance

Programme 3 was also based on three stages, but third selection stage took place after the bulls were progeny tested also for CP_m, on the basis of the calving records of their daughters. Selection proportions and index information for beef traits and CP_d were the same as in programme 2. In the first two stages selection index contained pedigree information for CP_m. In third stage, bulls index was based on calving records of 30 daughters and of 50 female half-sibs. For females own and half-sibs performance for CP_m was used in the index. Assumed generation interval was 63 mo for sires to sire and 38 mo for dams to sire.

Breeding programme 4 – specialised sire and dam lines

Programme 4 was based on the application of the theory of Smith (1964) who showed the advantage to cross specialised lines, selected for different traits, when the correlations between traits are negative. In this programme two lines, selected according different criteria, have been considered: the first line was a paternal beef line selected for beef traits and CP_d, whereas the second line was a maternal breeding line selected for all traits, including also CP_m. The commercial population to be slaughtered was obtained by crossing the two lines, whereas the pure lines were used to produce male and female parents of the next generation. The total number of bulls and cows selected per generation was the same as in previous programmes. However, the maternal breeding line accounted for 60% of the selected sires and dams per generation (12 bulls and 6000 cows). Higher resources in the use of performance testing facilities were reserved to the paternal beef line, accounting for 60% of the bulls tested in this stage.

Response to selection was calculated for the pure lines and for the commercial "crossbred" population according to Moav (1966). Response in the commercial population was the average of the responses obtained in the pure lines for the traits expressed by slaughter animals (DG, Flesh and CP_d) plus the response in the maternal breeding line for CP_m.

A summary of the characteristics of the breeding programmes is reported in Table 3.

Table 3. Breeding goal and index information for selection candidates in the simulated breeding programmes

	Breeding goal[a]	Index information[b]	
		Male candidates	Female candidates
Programme 1	DG	P + OP + HS	P + HS
	Flesh	P + OP + HS	P + HS
Programme 2	DG	P + OP + HS	P + HS
	Flesh	P + OP + HS	P + HS
	CP_d	P + OP + HS + (PR)	P + OP +HS
Programme 3	DG	P + OP + HS	P + HS
	Flesh	P + OP + HS	P + HS
	CP_d	P + OP + HS + PR	P + OP +HS
	CP_m	P + HS + (PR)	P + OP +HS
Programme 4			
Beef line	DG	P + OP + HS	P + HS
	Flesh	P + OP + HS	P + HS
	CP_d	P + OP + HS	P + OP +HS
Breeding line	DG	P + OP + HS	P + HS
	Flesh	P + OP + HS	P + HS
	CP_d	P + OP + HS + PR	P + OP +HS
	CP_m	P + HS	P + OP +HS

[a]*DG = daily gain; Flesh = live fleshiness; CP_d = direct calving performance; CP_m = maternal calving performance.*

[b]*P = pedigree information, OP = own performance, HS = half-sibs information, PR = progeny information, (PR) = progeny information may or may not be included depending on alternatives.*

 Response to selection

Programme 1

Response to selection per year obtained with breeding programme 1 is reported in Table 4. Response is expressed in genetic SD which enables an easier comparison of response between traits (see Table 2 for the value of one genetic SD in trait units). The economic values estimated by Albera et al. (2004a) indicated that the economic importance of DG was smaller than that of Flesh. Response to selection obtained in DG was very low compared to that for Flesh in the base situation. This was due to the low economic value and to the negative genetic correlation with Flesh (Albera et al., 2004b). However, by increasing the relative weight of DG in the index, it was possible to obtain more gain for this trait with a limited loss in the gain for Flesh. In alternative 1 the economic value of DG was increased by 50% to 0.32. Response to selection for DG was over five times as high as in the base situation, whereas for Flesh a 16% reduction was observed.

Table 4. Response to selection per year obtained in breeding programme 1

Trait [a]	Base[b]		Alternative 1[c]		Alternative 2[d]	
	Economic values, €/trait unit	Response to selection, genetic SD/yr	Economic values, €/trait unit	Response to selection, genetic SD/yr	Economic values, €/trait unit	Response to selection, genetic SD/yr
DG, g/d	0.21	0.009	0.32	0.048	0.32	0.053
Flesh, points	59.69	0.128	59.69	0.107	59.69	0.119
CP_d, points	----	0.032	----	0.049	----	0.055
CP_m, points	----	0.026	----	0.015	----	0.016

[a]*DG = daily gain; Flesh = live fleshiness; CP_d = direct calving performance; CP_m = maternal calving performance.*
[b]*Base: estimated economic values.*
[c]*Alternative 1: different economic values compared to base situation.*
[d]*Alternative 2: increased testing capacity compared to alternative 1.*

In general, the correlated response on calving performance was unfavourable, particularly for direct effect. It should be noted that for calving performance a positive response to selection is biologically unfavourable because, due to the scale adopted, high values are associated with increased calving difficulties. Giving more emphasis in the index to DG caused a better response in CP_m, but had a detrimental effect on CP_d due to the corresponding genetic correlations. Overall, selection for beef traits leads to an increase in calving problems by acting both on the calf and the dam components. The unfavourable response on calving performance increases when more emphasis is given to DG in the breeding goal.

The increase in the testing capacity for beef traits (alternative 3), obtained by doubling the size of the genetic station, caused a little improvement in the response in beef traits (+10%) and a moderate decline in calving performance.

Programme 2

Table 5 shows response to selection obtained in breeding programme 2. When estimated economic values were used, introduction of CP_d in the breeding goal caused a large negative response in DG, due to the strong unfavourable genetic correlations between DG and CP_d (Albera et al., 2004b). The corresponding effect for Flesh was moderate, as the response in this trait was around 20% less than that realised when only beef traits were selected.

Response to selection for CP_d was consistent. This was a consequence of the genetic independence between CP_d and Flesh, which has the highest economic importance in the index, in opposition to the antagonistic relationships that both traits have with DG. As expected, response in maternal calving performance was unfavourable due to the correlations with other traits.

In alternative 1 a restricted selection index was constructed in order to enable a slight positive response for DG. This caused a moderate reduction in the realised gain for CP_d and a marked decrease in that of Flesh (-27%). The favourable correlation with DG allowed a little improvement in the response for CP_m compared to the base situation.

The more accurate prediction of breeding values for CP_d, obtained by increasing the number of offspring per progeny tested sire from 100 to 200, produced a very limited effect on the response to selection for CP_d (alternative 2). This was probably a consequence of the low intensity of selection in the third stage of the programme, when progeny information was used in the index, in combination with the emphasis on beef traits in the breeding goal.

Table 5. Response to selection per year obtained in breeding programme 2

Traits[a]	Economic values, €/trait unit	Response to selection, genetic SD/yr		
		Base[b]		
DG, g/d	0.21	-0.036		
Flesh, points	59.69	0.102		
CP_d, points	-90.25	-0.048		
CP_m, points	----	0.046		
		Alternative 1[c]	Alternative 2[d]	Alternative 3[e]
DG, g/d	0.45	0.015	0.014	0.018
Flesh, points	59.69	0.074	0.074	0.089
CP_d, points	-160.00	-0.038	-0.040	-0.043
CP_m, points	----	0.042	0.041	0.059

[a]*DG = daily gain; Flesh = live fleshiness; CP_d = direct calving performance; CP_m = maternal calving performance.*
[b]*Base: estimated economic values.*
[c]*Alternative 1: different economic values compared to base situation.*
[c]*Alternative 2: increased progeny information for CP_d.*
[d]*Alternative 3: no progeny testing for CP_d.*

In alternative 3 the breeding values of bulls for CP_d were predicted based on own and half-sibs performance, without progeny testing. This allowed to reduce the generation interval of bulls to 26 mo as in programme 1, because the bulls were directly selected at the end of the performance test. As a consequence, obtained gains per year for beef traits and CP_d were consistently improved, even though the accuracy of the index was lower compared to the progeny testing scheme. Due to unfavourable direct-maternal genetic correlations (Carnier et al., 2000), the improvement of CP_d caused a marked negative effect on CP_m.

In general, compared to selection for beef traits only (breeding programme 1), the inclusion of CP_d in the breeding goal influenced the improvement of beef traits: particularly

response for DG was reduced by the introduction of the new trait, whereas the decrease in that for Flesh was moderate. The improvement of CP_d was counteracted by the strong unfavourable response obtained for CP_m, leading to an unfavourable change in the phenotypic expression of calving performance. The best strategy to select beef traits and CP_d proved to be the short scheme without progeny testing of bulls and the use of a selection index with rearranged economic values to avoid the negative response for DG. However, in the long term this strategy is not able to prevent the decline in calving performance inducted by selection for beef traits. As a consequence, the introduction of CP_m in the breeding goal is needed.

Programme 3

In breeding programme 3 response to selection in the base situation was unfavourable for DG and, particularly, for CP_m (Table 6). The antagonistic genetic correlations with CP_d and Flesh (Carnier et al., 2000; Albera et al., 2004b) and the low relative economic value (Albera et al., 2004a) were the reasons for this result. Gains in other traits were affected by the introduction of CP_m in the breeding goal: compared to programme 2, a decrease of 20% in the response to selection for Flesh was observed, for CP_d reduction approached 40%.

Some alternative selection indices have been developed by iterating on the relative economic values of traits, with the aim to obtain a more homogeneous response. The selection index used in alternative 1 allowed a favourable response in all traits. In this index the economic values of CP_m and Flesh have been substantially increased and reduced, respectively. The obtained gain for Flesh halved compared to the base situation. For CP_d response to selection was lower than in the base situation, but combined with that in CP_m, ensured an overall improvement of calving performance.

The accuracy of sires predicted breeding values for CP_d and CP_m was improved by increasing the progeny information up to 200 and 60, respectively (alternative 2). Selection of beef traits, taking place mainly at an earlier stage, was nearly not affected. The response to selection for CP_m was improved without any change in that of CP_d.

Response to selection was calculated simulating a short progeny testing scheme, enabling a reduction in the length of generation interval (alternative 3). In this scheme sires were progeny tested for CP_d only, whereas information about CP_m was provided by calving records of their female half-sibs. The lower accuracy of the index for CP_m was compensated by the shorter generation interval, which was similar to that of programme 2.

Table 6. Response to selection per year obtained in breeding programme 3

Traits[a]	Economic values, €/trait unit	Response to selection, genetic SD/yr		
		Base[b]		
DG, g/d	0.21	-0.021		
Flesh, points	59.69	0.080		
CP$_d$, points	-90.25	-0.028		
CP$_m$, points	-23.72	0.054		
		Alternative 1[c]	Alternative 2[d]	Alternative 3[e]
DG, g/d	0.17	0.006	0.006	0.008
Flesh, points	28.00	0.042	0.040	0.060
CP$_d$, points	-120.00	-0.014	-0.014	-0.024
CP$_m$, points	-80.00	-0.012	-0.017	0

[a]*DG = daily gain; Flesh = live fleshiness; CP$_d$ = direct calving performance; CP$_m$ = maternal calving performance.*
[b]*Base: estimated economic values.*
[c]*Alternative 1: different economic values compared to base situation.*
[d]*Alternative 2: increased progeny information both for CP$_d$ and CP$_m$.*
[e]*Alternative 3: no progeny testing for CP$_m$.*

A positive effect was observed for beef traits and CP$_d$, whose response to selection was markedly increased in comparison with that obtained in the conventional progeny testing scheme. This was a consequence of the faster generation turnover that, for these traits, was not associated to a reduction in the accuracy of the index. Response to selection for CP$_m$ was null, showing a substantial decrease compared to previous alternatives, due to the lower amount of information used in the index.

The general effect resulting from the introduction of CP_m among the selected traits was an important reduction in the gain of other traits: for beef traits the reduction ranged from 60% to 30% of the response obtained in programme 2, depending on the alternatives, for CP_d on average it halved.

The conventional progeny testing scheme (alternatives 1 and 2) allowed to improve calving performance, by acting both on direct and maternal components, and to obtain relatively low gain in beef traits. With the short progeny testing scheme (alternative 3) the overall response in calving performance was favourable but lower and obtained by improving CP_d only, while maintaining the current level for CP_m. However, as the selection for beef traits was much more effective than in previous alternatives, this scheme proved to be economically more efficient.

Programme 4

In this programme, the selection of specialised beef and breeding lines to be crossed to produce the commercial population was simulated. The paternal beef line was selected for beef traits and CP_d according to the criteria previously defined for alternative 3 of programme 2. In the maternal breeding line also CP_m was selected beside the other traits; for this line the scheme developed in alternative 3 of programme 3 was followed, but the economic weight of CP_m was slightly increased to improve the gain for this trait.

Estimates of response to selection in the commercial population and in the pure lines are presented in Table 7.

Table 7. Response to selection (genetic SD/yr) obtained in breeding programme 4 – commercial population and pure lines

	Traits[a]			
	DG, g/d	Flesh, points	CP_d, points	CP_m, points
Commercial population	0.017	0.069	-0.024	-0.021
Beef line	0.023	0.098	-0.032	0.057
Breeding line	0.011	0.039	-0.016	-0.021

[a]*DG = daily gain; Flesh = live fleshiness; CP_d = direct calving performance; CP_m = maternal calving performance.*

Compared to the single-line programme for the selection of all traits (programme 3), the two-line scheme increased markedly the response to selection in the commercial population especially for production traits, DG and Flesh. The overall response in calving performance was also improved, combining the gain obtained in the short progeny testing scheme for CP_d with that realized in the conventional progeny testing scheme for CP_m.

As in the breeding goal of the breeding line more emphasis was given to CP_m, the gain in this trait was higher than that in the single-line programme; as a consequence, due to genetic correlations, also gain in DG was higher. Similarly to the results of programme 2, in the beef line a very strong unfavourable effect on CP_m was observed, beside a considerable improvement of production traits. Even if not expressed in the commercial population, the decline in CP_m could affect the long term reproductive ability of the dams in the nucleus of this line.

Discussion

A simulation study was conducted to get more insight in the complex beef cattle breeding scheme. Some simplifications had to be made. Firstly, discrete generations have been considered in order to allow calculation of response to selection under multistage selection, whereas breeding programmes in cattle are structured with overlapping generations. After performance testing for beef traits, selection is practiced within contemporary groups of bulls on test formed by animals born in the same month (Albera et al., 2001). This selection within contemporary groups could not be accounted for in the simulated breeding programmes. Nevertheless, this study provided useful insight into the possibility of introducing calving performance in the breeding programme of Piemontese cattle.

The main limiting factor in the establishment of a selection procedure was the antagonistic genetic relationships among traits of interest. The antagonistic correlation between DG and CP_d proved to be the most important in restrictiong the response to selection, but also that between CP_d and CP_m was relevant.
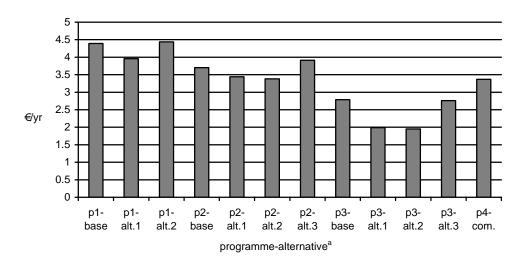
This study revealed that the simultaneous improvement of all considered traits was not realised using the economic values estimated by Albera et al. (2004a). The economic

selection index maximizes the overall economic response in the aggregate genotype (Hazel, 1943). However, when relevant negative genetic correlations exist or traits consistently differ in their economic importance, maximization of economic response may lead to no or negative response in some individual traits. A desired gain approach can be followed when a response in a specified direction is required in some of the traits (Brascamp, 1984). Gibson and Kennedy (1990) showed the superiority of objective indices, developed through the use of efficiency functions, over desired gain indices. However, for the breeders restrictions in the desired direction of change do exist which are not necessarily met by economic values. Small changes in economic values might result in a more balanced improvement of individual traits.

The economic selection index might not fit the particular situation represented in this study, as large negative correlations exist between traits, CP_d and CP_m, that contribute to the same phenotypic expression. In the economic selection index approach these traits are considered as simply correlated traits. As a consequence, no changes might result in phenotypic expression of calving performance, which is the combination of individual responses obtained in CP_d and CP_m.

The threshold nature of calving performance can complicate the establishment of an economic selection index including also other linear traits. The linear approach in the maximization of the aggregate genotype, which is used in the economic selection index, can lead to a favourable reponse in a threshold trait not large enough to change trait expression, because the threshold has not been reached. For these reasons, in this study the desired gain approach was choosen and realized by varying the economic values of traits in the breeding goal.

It is important to compare the set of economic values obtained developing desired gain indices with the set estimated using a bio-economic model. When these sets differs greatly, selection could be sub-optimal from an economic perspective. As a consequence, also in such situations, the use of bioeconomic models to derive index coefficients should be suggested to objectively evaluate the potential economic inefficiency of desired gain indices. Graph 3 reports the overall response to selection of the alternative programmes expressed in €/yr. Overall response was calculated weighting the obtained response in individual traits by the optimal set of economic values, corresponding to those estimated by bioeconomic modelling (Albera et al., 2004a).

[a]p1-base: programme 1 – estimated economic values.
p1-alt.1: programme 1 – alternative economic values.
p1-alt.2: programme 1 – increased testing capacity.
p2-base: programme 2 – estimated economic values.
p2-alt.1: programme 2 – alternative economic values.
p2-alt.2: programme 2 – increased progeny information for CP_d.
p2-alt.3: programme 2 – no progeny testing for CP_d.
p3-base: programme 3 – estimated economic values.
p3-alt.1: programme 3 – alternative economic values.
p3-alt.2: programme 3 – increased progeny information both for CP_d and CP_m.
p3-alt.3: programme 3 – no progeny testing for CP_m.
p4-com.: programme 4 – commercial population.

Graph 3. Overall economic response of simulated breeding programmes

Expressing the response to selection in economic units allows the evaluation of the economic loss due to the use of desired gain indices and also an easier comparison of the revenues of programmes. The desired gain approach led to a modest reduction of economic efficiency of selection in programme 1 and 2 (-10%), which increased to 28% when maternal calving performance was included in the breeding goal (comparison of alternative 1 vs base situation within each programme). The loss in programme 3 was due to the relatively large importance assigned to calving performance at expense of beef traits, in

order to obtain a favourable response in all traits. However, the loss could be overcome by reducing the generation interval in the short progeny testing scheme (alternative 3).

In general, ignoring calving performance in the breeding goal allowed a much higher response to selection in beef traits. The unfavourable correlations and the increase in the generation interval due to progeny testing limited the improvement of beef traits when calving performance was considered.

The choice of the selection strategy depends on the position of the considered beef breed on the market. If crossbreeding to dairy cattle is the main purpose, programme 2 has to be preferred because it allows for improvement in beef traits, while limiting calving problems by acting on the direct component. However, it should be considered that the revenues of such a programme will only be transferred to the elite purebred farmers involved in the programme by a proper payment for young bulls to be tested. For the majority of purebred farmers, the expected worsening of calving performance due to the unfavourable correlated response on maternal effect, will substantially increase husbandry costs. Therefore, it is questionable whether this strategy will turn into advantage of purebred farmers and consequently of the entire breed in the long term. Programme 3, considering also maternal calving performance in the breeding goal, avoids negative response in individual traits. In this programme, obtaining relatively high improvement in Flesh and CP_d, while restricting the negative correlated effect on DG and CP_m, was the most appropriate strategy also from an economic perspective. In order to maintain effectiveness of selection for beef production traits, the reduction of generation interval was crucial. Therefore, the scheme where the sires were progeny tested for CP_d only allowed to obtain the best result, combining a fast generation turnover with an acceptable accuracy of the predicted breeding values for all traits but CP_m. Index information for this trait were limited, but large enough to maintain the current genetic level in the population, while improving the other traits.

The selection of specialised paternal and maternal lines, selected with more emphasis on production and reproduction traits respectively, and the subsequent line breeding increased the genetic gain in most of the traits compared to the single-line programme. The two-line scheme allowed an overall economic response 20% higher than that obtained with programme 3 (Graph 3).

This scheme combined the benefits of programme 3, allowing to exploit the larger genetic gain in the commercial purebred population, with those of programme 2, providing a

paternal line very suitable for crossbreeding purposes. The advantage of the two-line scheme was due to the sire-dam heterosis (Moav, 1966), resulting from the unequal contribution to profit of paternal and maternal lines. The paternal line contributed to economic efficiency only through the production and reproduction traits, expressed by the commercial population (beef traits and CP_d), whereas in the maternal line also selection for reproductive traits (CP_m) affected profit.

However, there are some drawbacks that limit the application of the two-line programme. The selection of more lines requires higher investments and complicates the organisation and management of the programme. Furthermore, the benefit in terms of response to selection can be exploited only when there is a complete application of the programme at the commercial level, with a correct use of paternal and maternal lines. This implies that a clear distintion between the nucleus, multipliers and commercial segments is required, which is not always the case in beef cattle. In the Piemontese breed the social structure of farms, being of moderate size and integrating suckler cows and fattening production systems, does not match with this situation..

The use of reproduction technologies such as semen sexing and embryo transfer could increase the benefit of the two-line programme. Semen sexing could optimize the selection of breeding stock within line. The possibility to preselect the sex of offspring would improve the efficiency of mating outcome, producing a majority of animals of the desired sex in each line. This would reduce the costs of maintaining more lines. Beside the general effect of increasing selection intensity, embryo transfer could overcome the problems in the calving ability of the females in the nucleus of the paternal beef line, which are expected to increase due to the selection for production traits.

In this scheme breeding animals are selected within line based on their purebred performance. The effectiveness of such a type of selection is dependent on the correlation between purebred and crossbred performance, that has been reported to decline after several generations of purebred selection (Wei and Van der Steen, 1991). The inefficiency of pure line selection in exploiting non-additive genetic effects would be the reason of the decrease (Wei and Van der Steen, 1991). In this study, the existence of exploitable heterosis by dominance, that could increase the advantage of line breeding over the single-line scheme, has not been considered. However, the size of non-additive genetic effects should be limited, resulting from the crossing between lines that belong to the same population and will not be divergently selected.

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In conclusion, in order to obtain the improvement of calving performance, the breeding goal and the selection index must include both direct and maternal effects. A two-line scheme appears to be the most efficient technological solution to select beef traits and calving performance and might be implemented when the social structure of farms allows this. Alternatively, a traditional single line programme can be adopted which is more simple to apply, but also leads to a lower genetic gain.

Perspectives for the Piemontese breed

The market of the Piemontese breed faced a deep transformation in the last years. The difficulties in the beef trade, due to the B.S.E. disease, contributed to new opportunities for the Italian beef breeds. The quality attributes of the beef, the national origin, the ties with use of farm land and family work and the integrated production system, allowing to ensure easily the traceability of the production, improved the position of the Piemontese on the market. The new commercial outlet positively affected the prices in a period that was in general difficult for the beef market. The support of the herdbook Anaborapi, providing breed certification, was strategically important to support for this development.

The favourable situation should hold in the future, because the request for Piemontese animals is still increasing due to a positive trend in the supermarket sales, even if the beef market is progressively returning to its normal course as before the B.S.E. disease. A possible reduction in the importation of calves to be fattened from foreign countries, due to EU policies, could create a further expansion for the Piemontese breed. However, the possibilities to increase the production are restricted by the size of the population and the structure of the farms. Therefore, also in consideration of the higher cost price, the Piemontese breed is likely to mantain its position on the market in the short or medium term.

Also Piemontese farms faced a remarkable transformation over the years. The increase in herd size forced farmers to optimise the use of the available resources, shifting the main interest in animals from productivity to efficiency.

There is now the concern to improve calving performance both for its contribution to the economic efficiency of the farms (Albera et al., 2004a) and to sustainable breeding, through its effect on the quality of life for farmers and adaptability also to lower input production systems.

If the selection strategy aimed to improve beef production traits and calving performance will be succesfull, the perspectives of the Piemontese breed will certainly increase.

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Summary

Summary

Calving performance is a trait of relevant economic and social importance in beef cattle production systems.

The aim of this thesis was the development of a programme for the improvement of calving performance and beef traits through selection in the Italian Piemontese cattle population.

In order to accomplish this objective the breeding goal has been economically defined and the heritabilities of calving performance as well as those of the beef traits have been estimated. As a subsequent step, the genetic correlations between calving performance and beef production traits have been estimated. Finally, response to selection for the traits included in the breeding goal has been calculated by simulating alternative breeding programmes in order to define an appropriate selection strategy.

In Chapter 2 the breeding goal has been formulated using a deterministic bio-economic model simulating a Piemontese cattle farm. Economic values of selected traits, reflecting their economic importance, have been calculated as the marginal increase in the profit of the farm resulting from their genetic improvement. The sensitivity of estimated economic values to changes in the economic and production circumstances has been evaluated. Biological values, reflecting effieny in energy utilization, have been calculated and compared with corresponding economic values.

Obtained results indicated the economic importance of calving performance and live fleshiness. Notwithstanding the lower incidence of dystocia in cows compared to heifers, the economic values of calving performance in later parities was almost four times higher in later parities than in the first parity. This was a consequence of the herd composition as in Piemontese herds on average only 20% of breeding females are first parity heifers. The economic value of daily gain was proportionally reduced compared to that of other traits, due to the increase in maintenance costs of animals resulting from a higher growth level. Estimated economic values were robust towards changes in production or economic scenarios; only the introduction of a quota system on beef production or energy consumption would require their redefinition. Biological values agreed with economic values for most of the investigated traits, indicating that the economic and energy utilization efficiency are well related in the analyzed production system.

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Genetic parameters for calving performance have been estimated using an animal model and considering first and later parities as different traits (Chapter 3). Calving performance is affected by a direct additive genetic effect, related to the calf genotype, and a maternal additive genetic effect, related to the dam genotype. These two effects have been included in the statistical model used to analyse calving performance assuming the existence of a correlation between them. Estimated values for heritability of the direct effect were 0.19 and 0.09 in the first and in later parities, respectively. Corresponding values for maternal effect were 0.08 and 0.05. Genetic variation of both effects was moderate but large enough to allow improvement through selection. Direct and maternal effects showed a strong negative genetic correlation (around -0.5, depending on parity), which might complicate the establishment of a selection procedure. Correlations between direct or maternal effects in the first and subsequent parities were very high (over 0.9). However, due to heterogeneity of estimated genetic variances, calving performance in first and later parities should be considered as different traits.

In Chapter 4 genetic parameters for beef production traits recorded during the performance testing on station have been estimated. Overall daily live-weight gain at the station was highly heritable (0.60), whereas live fleshiness traits appraised through morphological evaluation showed moderate to high heritabilities, ranging from 0.34 to 0.55 depending on the considered part of the body. Evaluations of live fleshiness traits were adjusted for the weight at scoring in order to provide a measure of muscular development independent of body size. As a consequence, the genetic correlation between daily live-weight gain and live fleshiness traits was negative (-0.25). Live fleshiness traits were highly correlated with each other, suggesting that the use of multiple trait models should be preferred in order to obtain more accurate prediction of sire's breeding values.

Differently from dairy cattle, calving performance and production traits cannot be considered genetically independent in beef cattle. The relationship between calving performance and beef traits have been investigated in Chapter 5. Genetic correlations have been estimated by the joint analysis of data collected in the farms on sires progeny (calving performance records) and data collected in the genetic station on sires directly (daily gain and live fleshiness). As a consequence, correlations have been mainly estimated through pedigree information.

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Daily gain showed a relevant antagonistic relationship with direct calving performance and a moderate favourable correlation with maternal calving performance. Selection for growth increases calves weight and but it also improves the calving ability of females. However, due to the magnitude of genetic correlations, a general decline in calving performance is expected as a net effect of such selection. Live fleshiness traits were poorly correlated with direct calving performance and showed unfavourable correlations with maternal calving performance. Therefore, cows showing strong muscular development are expected to calve with more problems, probably due to a reduction in the size of their pelvic area. Estimated genetic correlations with beef traits were similar for first or later parities calving performance.

The existence of conflicting genetic relationships between production traits and calving performance required the development of a specific selection strategy, which was studied in Chapter 6. Deterministic simulation of breeding programmes has been used to calculate response to selection under different scenarios. The economic values and genetic parameters estimated in previous chapters have been used in the simulation study. Breeding programmes differed in the traits included in the breeding goal: beef traits only, beef traits and direct calving performance, beef traits and direct and maternal calving performance. The use of specialized paternal and maternal lines selected according different breeding goals was also considered.

Due to unfavourable genetic correlations, selection for beef traits caused a strong negative effect on both direct and maternal calving performance. Selecting for direct calving performance and beef traits did not prevent an increase of calving problems, as the reduction in the size of calves gain was overwhelmed by the decline in calving ability of cows. When the breeding goal also included maternal calving performance a considerable reduction in realized genetic gain for beef traits was observed. Furthermore, the simultaneous improvement of all considered traits was not obtained using the estimated economic values. A desired gain approach in the establishment of the selection index enabled the improvement of beef traits and direct calving performance while maintaining the current genetic level of the population for maternal calving performance. Hence, the improvement of phenotypic expression of calving performance could only be achieved by including direct and maternal effects both in the breeding goal and in the index. Strategies allowing a reduction of generation interval proved to be crucial to allow genetic gain for beef traits.

The selection of specialized paternal and maternal lines to be crossed increased the overall economic response of 20%. The unequal paternal and maternal contributions caused a larger genetic gain in beef traits and maternal calving performance compared to alternative programmes. However, the application of such a programme could be limited by the structure of the production system, particularly in terms of farm size.

In conclusion, the specialized lines programme is the recommended strategy to select beef traits and calving performance, when allowed by the social structure of farms. In alternative, a single line programme, including direct and maternal calving performance beside beef traits, can be used. In this case, compared with the specialized lines programme, more flexibility for the application of the programme but also lower economic revenues have to be expected.

Riassunto

Riassunto

La facilità di parto è un carattere economicamente e socialmente importante nell'allevamento dei bovini da carne.

La finalità di questa tesi è stata la definizione di una strategia per il miglioramento della facilità di parto e degli altri caratteri legati alla produzione di carne, attraverso la selezione genetica, nella razza bovina Piemontese.

Tutto ciò ha comportato ha comportato la formulazione di un obiettivo di selezione, la stima dei parametri genetici relativi ai caratteri selezionati ed infine la stima della risposta alla selezione ottenibile applicando programmi selettivi diversi, al fine di indentificare la strategia selettiva più vantaggiosa.

Nel Capitolo 2 della tesi, gli obiettivi di selezione sono stati definiti economicamente attraverso un modello deterministico di simulazione bio-economica dell'allevamento di bovini Piemontesi. Accanto alla facilità di parto, considerata come un diverso carattere nelle primipare e nelle pluripare, sono stati inseriti tra gli obiettivi di selezione caratteri legati alla produzione di carne quali l'accrescimento e la muscolosità.

Attraverso il modello sono stati derivati i valori economici dei caratteri selezionati, che sono funzione del profitto determinato dall'incremento marginale di ognuno di essi ottenuto per effetto del miglioramento genetico. E' stata studiata la sensitività dei valori economici stimati rispetto a possibili cambiamenti nello scenario economico e nelle caratteristiche produttive degli allevamenti. Inoltre, si è proceduto al calcolo dei valori biologici dei caratteri studiati, che sono legati all'incremento di efficienza nell'utilizzo dell'energia indotto dalla selezione. La comparazione dei valori biologici ai corrispondenti valori economici ha consentito di giungere ad una più completa valutazione dell'importanza relativa dei caratteri selezionati.

I risultati ottenuti hanno evidenziato la rilevanza economica della facilità di parto e della muscolosità. A dispetto della ridotta incidenza dei problemi di parto nelle vacche adulte rispetto alle manze, il valore economico della facilità di parto nelle pluripare è stato circa quattro volte più alto rispetto a quello nelle primipare. Ciò è dovuto al fatto che la quota di primipare presenti nell'allevamento è pari al 20% circa delle bovine e quindi ha un impatto relativamente limitato sui costi dovuti alle distocie. Per quanto riguarda l'accrescimento, il valore economico stimato è stato proporzionalmente inferiore a quello

degli altri caratteri a causa dell'effetto negativo sui costi di mantenimento degli animali indotto dalla maggiore velocità di crescita. I valori economici stimati hanno dimostrato buona robustezza rispetto a possibili cambiamenti nello scenario economico e produttivo: solamente in caso di istituzione di un regime di quota sulla produzione di carne o sul consumo di energia per l'alimentazione i valori stimati dovrebbero essere adattati. I valori biologici sono risultati in accordo con quelli economici per la maggior parte dei caratteri considerati, evidenziando che, nel sistema produttivo analizzato, esiste una buona corrispondenza tra miglioramento dell'efficienza economica e miglioramento dell'efficienza di utilizzo dell'energia.

I parametri genetici per la facilità di parto sono stati stimati utilizzando un modello animale e considerando i parti delle bovine primipare e quelli delle bovine pluripare come caratteri diversi (Capitolo 3). La facilità di parto è influenzata da effetti genetici additivi diretti, legati al genotipo del vitello, e da effetti genetici additivi materni, legati al genotipo della bovina. I due effetti sono stati pertanto inclusi nel modello statistico utilizzato per l'analisi dei dati di parto, assumendo l'esistenza di una correlazione tra loro. I valori di ereditabilità ottenuti sono stati pari a 0.19 e 0.09 per l'effetto diretto, rispettivamente nelle primipare e nelle pluripare. I corrispondenti valori per l'effetto materno sono stati 0.08 and 0.05. La varabilità genetica esistente per entrambi gli effetti è risultata moderata, ma sufficientemente ampia da essere sfruttabile attraverso la selezione. Gli effetti diretti e materni hanno mostrato una correlazione genetica negativa abbastanza importante tra loro (intorno a -0.50), che potrebbe complicare lo sviluppo di una strategia selettiva. Le correlazioni genetiche stimate tra gli effetti diretti o materni nei parti delle primipare ed in quelli delle pluripare sono risultate molto alte, con valori oltre 0.9. Tuttavia, a causa della etereogeneità delle varianze stimate, la facilità di parto nelle manze e nelle vacche adulte dovrebbero essere considerate come caratteri diversi dal punto di vista genetico.

Nel Capitolo 4 sono stati stimati i parametri genetici dei caratteri legati alla produzione di carne, misurati durante la prova di performance in stazione. L'ereditabilità dell'accrescimento è stata molto elevata (0.60). I caratteri relativi alla muscolosità degli animali, rilevati attraverso la valutazione morfologica, hanno presentato valori di ereditabilità da medi ad elevati (da 0.34 a 0.55, a seconda della regione corporea). Le valutazioni della muscolosità sono state aggiustate in funzione del peso alla valutazione, in

modo tale da costituire una misura della conformazione da carne indipendente dalle dimensioni dell'animale. Conseguentemente, la correlazione genetica stimata tra l'accrescimento ed i caratteri di muscolosità è risultata mediamente negativa (-0.25). Dal momento che i vari caratteri di muscolosità hanno presentato correlazioni molto elevate tra loro, l'utilizzo di modelli multivariati per la loro analisi consente di ottenere indici genetici più accurati.

A differenza di quanto avviene nei bovini da latte, la facilità di parto ed i caratteri produttivi non possono essere considerati geneticamente indipendenti nei bovini da carne. Le relazioni genetiche tra facilità di parto e caratteri legati alla produzione di carne sono state studiate nel Capitolo 5. Le correlazioni genetiche sono state stimate analizzando congiuntamente dati rilevati nelle aziende sulla progenie dei tori (codici di parto), con dati rilevati in stazione direttamente sui tori (accrescimento e muscolosità). Come conseguenza, le correlazioni sono state stimate prevalentemente attraverso le relazioni di parentela tra gli animali. L'accrescimento ha evidenziato relazioni conflittuali importanti con la facilità di parto diretta e correlazioni favorevoli con la facilità di parto materna. La selezione per l'accrescimento determina un aumento del peso alla nascita dei vitelli, ma nello stesso tempo migliora l'attitudine al parto delle bovine. Tuttavia, a causa dell'entità delle correlazioni genetiche, l'effetto netto di un tale tipo di selezione è un peggioramento della facilità di parto nel suo complesso. La muscolosità ha mostrato correlazioni deboli con la facilità di parto diretta e mediamente antagoniste con la facilità di parto materna. Quindi, le bovine con masse muscolari molto sviluppate tendono a partorire con maggiori problemi, probabilmente a causa di una riduzione nelle dimensioni dell'area pelvica. Le correlazioni stimate con i caratteri carne sono risultate simili per la facilità di parto nelle primipare e nelle pluripare.

L'esistenza di rapporti genetici conflittuali tra caratteri produttivi e facilità di parto ha richiesto la messa a punto di una strategia selettiva appropriata, che è stata studiata nel Capitolo 6. Sono state adottate simulazioni di tipo deterministico per calcolare la risposta alla selezione ottenibile con schemi selettivi alternativi, utilizzando i parametri genetici ed economici stimati in precedenza. Gli schemi selettivi simulati presentavano differenze nei caratteri considerati: sono state simulate la selezione dei soli caratteri carne, quella dei caratteri carne e della facilità di parto diretta ed infine quella dei carateri carne e della

facilità di parto diretta e materna. Inoltre si è simulato uno schema di selezione articolato in due diverse linee selettive, paterna e materna, selezionate in base a criteri differenti.

A causa delle correlazioni genetiche, la selezione per i soli caratteri legati alla produzione di carne ha determinato una forte risposta correlata negativa sulla facilità di parto diretta e materna. La selezione della facilità di parto diretta e dei caratteri carne non è stata sufficiente a prevenire un incremento dei problemi al parto: la riduzione del peso alla nascita dei vitelli è stata infatti controbilanciata da una riduzione nell'attitudine al parto delle bovine. L'inclusione tra gli obiettivi di selezione anche della facilità di parto materna ha determinato una sensibile riduzione del miglioramento ottenuto per i caratteri legati alla produzione di carne. Inoltre, utilizzando i valori economici stimati, non è stato possibile ottenere una risposta positiva in tutti i caratteri. L'utilizzo di un indice di selezione per un guadagno predeterminato (desired gain index) ha consentito di ottenere un miglioramento dei caratteri carne e della facilità di parto diretta, mantenendo l'attuale livello della facilità di parto materna nella popolazione. Quindi, il miglioramento dell'espressione fenotipica della facilità di parto è stato possibile solamente quando gli effetti diretti e materni della stessa sono stati inclusi sia negli obiettivi di selezione che nell'indice. Le strategie volte al contenimento dell'intervallo di generazione sono infine state fondamentali per garantire una risposta alla selezione positiva per i caratteri legati alla produzione di carne.

La selezione di linee paterne e materne specializzate ed il successivo loro incrocio hanno determinato una risposta economica superiore del 20% a quella degli schemi tradizionali. Il diverso contributo delle linee paterne e materne ha consentito una maggiore risposta alla selezione nei caratteri carne e nella facilità di parto materna rispetto agli altri schemi. Tuttavia, l'applicazione dello schema selettivo basato sulle due linee potrebbe trovare delle limitazioni dovute alla struttura del sistema produttivo: una programma di selezione di questo tipo richiede infatti dimensioni aziendali ampie.

In conclusione, lo schema basato sulle due linee selettive specializzate si configura come la strategia raccomandabile per la selezione dei caratteri carne e della facilità di parto, quando la struttura delle aziende e del sistema produttivo lo consentono. In alternativa può essere utilizzato uno schema selettivo tradizionale, basato su un'unica linea e che includa la facilità di parto sia diretta che materna a fianco dei caratteri carne. In questo caso, rispetto allo schema con le due linee selettive specializzate, il programma si presenta più flessibile e facile da applicare ma anche in grado di produrre una risposta alla selezione inferiore.

Samenvatting

Samenvatting

Selectie op vleesproductie-eigenschappen en geboorteverloop in het Piemontese ras

Het doel van dit proefschrift was de ontwikkeling van een fokprogramma voor de verbetering van geboorteverloop en vleesproductie-eigenschappen in het Italiaanse rundveeras Piemontese. Om dit fokprogramma te ontwikkelen is het (economisch) fokdoel berekend en is de mate van erfelijkheid (erfelijkheidsgraad) van zowel geboorteverloop als vleesproductie-eigenschappen geschat. Vervolgens zijn de genetische verbanden (ofwel correlaties) tussen geboorteverloop en vleesproductie-eigenschappen geschat. Met deze gegevens zijn verwachte genetische vooruitgangen berekend voor geboorteverloop en vleesproductie-eigenschappen onder verschillende, alternatieve fokprogramma's. Op basis van deze uitkomsten is een voor de praktijk gewenst fokpogramma ontwikkeld.

Fokdoel

Het fokdoel is berekend, gebruikmakend van een zogenaamd biologisch-economisch simulatie-model van een vleesveebedrijf met Piemontese dieren. Economische waarden van eigenschappen zijn berekend als de marginale toename in winst van het bedrijf als gevolg van een marginale verhoging van de genetische aanleg van de aanwezige dieren. De gevoeligheid van deze economische waarden voor aannames in de simulatie ten aanzien van economische omstandigheden (als prijzen van producten) en andere productie-omstandigheden (als niveau van productie) is geëvalueerd. Daarnaast is ook gekeken naar 'biologische waarden': in hoeverre verandert de benutting van energie als gevolg van de verhoging van de genetische aanleg.

De verkregen resultaten wijzen vooral op het economische belang van de verbetering van geboorteverloop en bevleesdheid van de dieren. Ondanks de lagere frequentie van het optreden van problemen in het geboorteverloop bij oudere-kalfskoeien in vergelijking met eerste-kalfskoeien (vaarzen) was de economische waarde van geboorteverloop in oudere-kalfskoeien toch bijna vier keer zo hoog. Dit is een direct gevolg van de samenstelling van de veestapel: op Piemontese bedrijven is maar ongeveer een vijfde van de koeien eerste-kalfs.

In de rundvleesproductie levert een hogere groei ook zwaardere dieren voor de slacht, en daarmee een hogere opbrengst. Maar de economische waarde van groei neemt relatief af

ten opzichte van andere kenmerken wanneer in de simulatie rekening gehouden wordt met de toename in voerkosten voor onderhoud van de moederdieren (koeien) op het bedrijf. Berekende (relatieve) economische waarden bleken tamelijk ongevoelig voor veranderingen in economische en andere productie-omstandigheden. Grote veranderingen in (relatieve) economische waarden treden alleen op bij de introductie van een bedrijfsquotering (fictieve vaststaande hoeveelheid) voor de totale vleesproductie-omvang of van de totale opname van voer-energie. Biologische waarden en economische waarden kwamen voor de meeste eigenschappen overeen, hetgeen aangeeft dat een selectie op economische waarden ook een verbetering van de energiebenutting geeft in de gesimuleerde productiesystemen.

Erfelijkheidsgraden en correlaties

Met behulp van een zogenaamd statistisch *animal model* ('diermodel') zijn uit geregistreerde praktijkgegevens genetische parameters (erfelijkheidsgraden en correlaties) geschat voor geboorteverloop. Daarbij zijn geboorteverloop in eerste pariteit (eerste-kalfskoeien) en latere pariteit als verschillende kenmerken gemodelleerd. Tevens is in het model aangenomen dat geboorteverloop beïnvloed wordt door een zogenaamd 'direct additief genetisch' effect, bepaald door het genotype van het kalf, en een zogenaamd 'maternaal additief genetisch' effect bepaald door het genotype van de moeder. Deze twee eigenschappen hebben een onderlinge (genetische) correlatie. De geschatte erfelijkheidsgraad voor het direct additief genetisch effect was 0,19 (ofwel, 19 % van de phenotypische verschillen in de geregistreerde praktijkgegevens is statistisch te herleiden tot genetische verschillen tussen individuele, onverwante dieren) voor eerste pariteit en 0,09 voor latere pariteiten. Voor het maternaal additief genetisch effect waren de schattingen 0,08 en 0,05 voor respectievelijk eerste en latere pariteit. De omvang van de geschatte genetische variatie van beide (direct en maternaal) genetische effecten was matig, maar groot genoeg om verbetering door selectie mogelijk te laten zijn. Het direct en het maternaal additief genetisch effect hebben een sterk negatieve genetische correlatie; ongeveer -0,5 (afhankelijk van pariteit). Dit compliceert naar verwachting de selectie in een fokprogramma. Immers, statistisch gezien heeft een vrouwelijk kalf dat zelf zonder problemen geboren wordt een grotere kans om later als moederdier met problemen in het geboorteverloop nakomelingen te krijgen. Geschatte genetische correlaties tussen direct additief genetische effecten in opeenvolgende pariteiten onderling en geschatte genetische correlaties tussen maternaal additief genetische effecten in opeenvolgende pariteiten onderling waren zeer hoog

(ongeveer 0,9). Toch moeten we deze eigenschappen in opeenvolgende pariteiten als verschillend beschouwen vanwege de verschillen in de hoogte van de genetische varianties.

Vleesproductie-eigenschappen worden geregistreerd tijdens een prestatie-toets voor stieren op een zogenaamd opfokstation. De eigenschap 'totale groei' tijdens de toetsperiode heeft een hoge geschatte erfelijkheidsgraad van 0,6. Bevleesdheid wordt tijdens de toets bepaald door deskundige inspecteurs aan de hand van waarnemingen aan verschillende lichaamsdelen van het levende dier. Bevleesdheidseigenschappen hebben een matig tot hoge geschatte erfelijkheidsgraad, variërende van 0,34 tot 0,55, afhankelijk van het bekeken lichaamsdeel van de dieren. In deze berekeningen is de waarneming voor bevleesdheid modelmatig gecorrigeerd voor het gewicht van het dier op het moment van de waarneming om zodoende een beter zicht te krijgen op de spierontwikkeling onafhankelijk van de totale lichaamsontwikkeling. De geschatte genetische correlatie tussen (dagelijkse) groei en bevleesdheid was negatief (-0,25) hetgeen mede gezien kan worden als een gevolg van de gehanteerde wijze van modelleren. Bevleesdheidseigenschappen hebben onderling een hoge genetische correlatie. Daaruit mag worden afgeleid dat het de voorkeur heeft om bij de fokwaardenschatting voor individuele stieren gebruik te maken van *multiple-trait* modellen (gelijktijdig analyseren van waarnemingen aan meerdere eigenschappen) om zodoende de nauwkeurigheid van de fokwaardenschatting te verhogen.

Anders dan bij melkvee, kan bij vleesvee niet gesteld worden dat geboorteverloop en productie-eigenschappen genetisch onafhankelijk overerven. Het onderzoeken van deze genetische correlatie is moeilijk, omdat de waarnemingen voor geboorteverloop plaatsvinden op praktijkbedrijven onder de nakomelingen van de stieren terwijl de waarnemingen voor vleesproductie-eigenschappen plaatsvinden aan de stieren zelf op de opfokstations. Hierdoor zijn de statistische schattingen voor een belangrijk deel gebaseerd op gemodelleerde genetische relaties tussen de dieren in de gegevenssets.

Groei blijkt een ongunstige correlatie te hebben met direct additief genetische effecten voor geboorteverloop – ofwel dieren die harder kunnen groeien hebben een grotere kans moeilijker geboren te worden. Daarentegen hebben koeien met een hogere groei minder kans op problemen wanneer ze zelf een kalf krijgen. Het totale effect bij deze onderlinge correlaties is dat een eenzijdige selectie op groei tot een toename in percentage moeilijke geboorten in Piemontese vee leidt. Bevleesdheid heeft nauwelijks een samenhang met direct

additief genetische effecten voor geboorteverloop, maar laat duidelijke ongunstige samenhang zien met maternaal additief genetische effecten. Ofwel, koeien met een hoge mate van bevleesdheid hebben naar verwachting meer problemen wanneer ze afkalven, waarschijnlijk als gevolg van een afname van de effectieve ruimte van het geboortekanaal. Geschatte correlaties voor bevleesdheid en geboorteverloop waren vergelijkbaar voor eerste en latere pariteits koeien.

Fokprogramma

De gevonden, je zou kunnen zeggen 'conflicterende', genetische correlaties tussen vleesproductie-eigenschappen en geboorteverloop vragen om een specifieke opzet van een fokprogramma. Daarom zijn voor verschillende scenario's verwachte genetische vooruitgangen berekend, gebruikmakend van eerder bepaalde fokdoel en genetische parameters. De scenario's verschilden in de definitie van het fokdoel: alleen vleesproductie-eigenschappen, vleesproductie-eigenschappen plus direct additief genetische effecten voor geboorteverloop, vleesproductie-eigenschappen plus zowel direct als maternaal additief genetische effecten voor geboorteverloop. Daarbij is ook gekeken naar een scenario met gespecialiseerde vaderlijnen en moederlijnen.

Als een gevolg van de ongunstige genetische correlatie tussen de kenmerken, heeft eenzijdige selectie op vleesproductie-eigenschappen een sterk negatief effect op geboorteverloop. Aanvullende selectie op direct additief genetische effecten voor geboorteverloop (naast selectie op vleesproductie-eigenschappen) geeft weliswaar een lagere genetische vooruitgang voor groei van de dieren, maar dit wordt tenietgedaan door de ongunstige effecten van kleinere koeien op geboorteverloop. Een aanvullende opname van maternaal additief genetische effecten in het fokdoel gaat vervolgens gepaard met een aanzienlijke afname in de genetische vooruitgang voor vleesproductie-eigenschappen. Daar komt bij, dat het gebruik van de volledige set van economische waarden zoals eerder berekend, niet een gelijktijdige gunstige genetische vooruitgang (lees: verbetering) van alle meegenomen kenmerken geeft. Met behulp van de '*desired gain*' benadering is het wel mogelijk om een fokdoel te definiëren met een set van economische waarden die een gunstige genetische vooruitgang geeft voor vleesproductie-eigenschappen en direct additief genetische effecten voor geboorteverloop onder een constant houden van de maternaal genetische effecten voor geboorteverloop (nul-groei). Een vermindering in de waar te

nemen incidentie van geboorteproblemen kan alleen bereikt worden bij een opname van additief en maternaal genetische effecten in het fokdoel en bij registratie van zowel waarnemingen aan geboren nakomelingen en aan afkalvende dochters van stieren. Scenario's met een korter generatie-interval (gebruik van jongere stieren als fokstier) laten duidelijk hogere genetische vooruitgangen zien voor vleesproductie-eigenschappen.

Wanneer we selectie op vleesproductie-eigenschappen loskoppelen van selectie op geboorteverloop door deze in verschillende groepen dieren te laten plaatsvinden, kunnen we gespecialiseerde vaderlijnen en moederlijnen fokken. Voor het verkrijgen van nakomelingen voor de vleesproductie kruisen we dan dieren uit de vader- en moederlijn. Dit geeft voor het totale systeem een verhoging van de genetische respons, in geld uitgedrukt plus 20%. Binnen de vaderlijn wordt (met een fokprogramma met een kort generatie-interval) een hogere genetische vooruitgang voor vleesproductie-eigenschappen behaald. In de moederlijn vindt een gecombineerde selectie plaats met een beperkte vooruitgang in vleesproductie-eigenschappen en gunstig vooruitgang voor geboorteverloop. De praktische toepassing van zo'n kruisingssysteem stelt wel specifieke eisen aan de sociale structuur van de vleesveehouderij-sector, en in het bijzonder aan de bedrijfsomvang.

Samenvattend, de studie geeft aan dat een fokprogramma met gespecialiseerde vaderlijnen en moederlijnen aan te bevelen is. Een dergelijk kruisingssysteem moet wel passen bij de sociale structuur van de vleesveehouderij-sector. Een alternatief is een fokprogramma met één fokpopulatie – dit is flexibeler, maar geeft wel lagere economische opbrengsten.

List of publications

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Curriculum Vitae

Andrea Albera was born on July 12th 1966 in Torino, Italy. After completing secondary education, he obtained a five years Degree in Agricultural Science with major in Animal Science at the University of Torino in 1993. After his Degree, he was employed by the Italian Piemontese cattle Breeders Association (ANABORAPI) to work as geneticist at the Research and Development Office. While working, he continued his education attending specialization courses in animal breeding at the University of Padova and Istituto Lazzaro Spallanzani, in Italy. In 1998 he joined the Animal Breeding and Genetics Group at Wageningen University and spent a period of 4 months attending MSc Courses in animal breeding and doing research on calving ease in cattle under the supervision of Dr. Ab Groen. In 1999 he started his PhD project in Animal Breeding at Wageningen University, which he combined with activities at ANABORAPI. Since 1999, he is Manager of the Research and Development Office of ANABORAPI, with the responsibility of breeding values estimation and selection strategies for Piemontese cattle. He is involved as a teacher in national awarded Professional Training Courses for Veterinarians. He is geneticist consultant of the Health Department of the Piemonte Region, lecturer for Animal Breeding courses at the University of Torino and referee for the Italian Journal of Animal Science.

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