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**REVIEW ARTICLE**

**Issues and perspectives in dairy sheep breeding**

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**ABSTRACT**

The present review consists of two parts. In the first part, the authors briefly describe the state of the art of breeding programmes for Italian dairy sheep; then they report new models for genetic evaluation and consider the problem of genotype x environment interaction and the impact of farming systems on the genetic merit of animals. In the second part new breeding goals regarding the evolution of milk quality concept and the increasing importance of functional traits are reported. Regarding milk quality, the authors especially focus on the traits related to cheese-making ability and on the nutraceutical aspects of milk. Among functional traits, resistance to diseases (mastitis and Scrapie) has been highlighted for its great importance in livestock species. Finally, the perspectives of marker-assisted selection have also been reported.

**Key Words:** Dairy sheep, Genetic improvement, Breeding goals, Milk quality, Functional traits

**RIASSUNTO**

ATTUALITÀ E PROSPETTIVE NEL MIGLIORAMENTO GENETICO DEGLI OVINI DA LATTE

La rassegna bibliografica è divisa in due parti. Nella prima vengono illustrati brevemente gli schemi di selezione attualmente adottati nelle principali razze ovine da latte italiane mettendone in evidenza i principali punti di forza e di debolezza. Successivamente vengono riportati alcuni modelli alternativi che potrebbero essere adottati nell’ambito degli attuali schemi di selezione e viene analizzata la problematica relativa all’interazione genotipo – ambiente nella definizione del merito genetico dei riproduttori, soprattutto nelle aree di allevamento marginali. Nella seconda parte gli autori trattano della definizione di nuovi obiettivi di selezione, prendendo in considerazione gli aspetti legati ai nuovi concetti di qualità del latte e all’introduzione dei caratteri funzionali nei modelli genetici di stima dei riproduttori. Per quanto riguarda la qualità del latte, è stato dato rilievo soprattutto alle caratteristiche del latte legate all’attitudine alla caseificazione e alle proprietà nutraceutiche del latte stesso. Relativamente ai caratteri funzionali, un particolare rilievo è stato dato alla resistenza alle malattie quali le mastiti e la Scrapie. Infine sono state riportate anche le recenti acquisizioni in merito alle possibilità offerte dalla selezione assistita dai marcatori.

**Parole chiave:** Pecore da latte, Miglioramento genetico, Obiettivi di selezione, Qualità del latte, Caratteri funzionali.
Introduction

In recent years there has been a marked increase in the interest in dairy sheep, both by researchers and members of the dairy industry. This attention has obviously been centred on Mediterranean countries, where most dairy ewes are farmed and two-thirds of the entire world’s sheep milk are produced (Table 1), but it can be also observed in countries that do not possess a sheep dairying heritage. This is the case, for example, of the USA, which imports significant amounts of dairy products (Thomas, 1994), or Germany, where a national breeding programme for milk sheep has recently been developed (Zumbach and Peters, 2003). The main reasons are probably the absence of production quotas, the enlargement of dairy sheep product markets and the opportunity to exploit marginal areas by low-input dairy sheep farming systems.

Present Mediterranean dairy sheep breeds are the result of either crossbreeding or purebred selection carried out on autochthonous multipurpose populations (Barillet, 1997). The main reason for converting local breeds into more specialised types has been the relative economic relevance of milk yield income on meat (ratio approximately 3:1). The relative impact of the two genetic strategies has been different among countries. A crossbreeding programme with East Friesian rams started in the early ‘70s in Italy for the Sarda breed, but results were rather unsatisfactory, as crossbred ewes are slightly more productive but markedly less profitable than purebred Sarda ewes (Sanna et al., 2001). Experiments on the Lacaune breed in France with East Friesian rams were stopped when it became clear that the time needed to spread foreign genes (up to the 75%, which was found to be the optimum percentage) in the French population was more or less comparable with the time needed to reduce the milk yield gap between the two genotypes (Barillet et al., 2001a). On the other hand, almost 45% of dairy sheep stock in Spain consists of foreign breeds, such as Awassi and Lacaune, or crosses that have replaced local breeds in semi-intensive or intensive farming systems (Ugarte et al., 2001).

Operating breeding programmes for dairy sheep exist in France, Italy and Spain, essentially based on the conventional scheme of the dairy cow. Basic elements are:

a) pyramidal structure of the breed, with an active population represented by animals involved in the selection programme at the top, and the remaining commercial population below;

b) existence of a milk performance testing scheme and registration of genetic relationships among animals;

c) artificial insemination as the main reproductive technique;

d) genetic evaluation of males based mainly on progeny test;

e) programmed matings according to the four traditional selection pathways (sires of rams, dams of rams, sires of ewes, dams of ewes).

An example of the structure of the breeding programme in the Lacaune and Sarda breeds is reported in Table 2.

Dairy sheep breeding programmes demonstrate a marked juvenile connotation in comparison to those of dairy cattle: all proven rams are used as sires of rams, whereas young rams are used as sires of ewes, in order to maintain a reasonable selection intensity in the male path and to reduce to 2-3 years the generation interval between sires and daughters in the schemes of Lacaune and Sarda, (Pagnacco and Sanna, 1995). However, application of the conventional scheme requires an adequate size and structure of the breeds. In Italy, for example, although there are 8 officially recognized dairy sheep breeds for which

Table 1. Dairy sheep stocks of Mediterranean countries.

| Country | N. of ewes |
|---------|-----------|
| Italy   | 6,147,500 |
| France  | 1,349,000 |
| Greece  | 9,268,000 |
| Israel  | 46,200    |
| Portugal| 500,000   |
| Spain   | 3,233,000 |
| Tunisia | 27,000    |
a herd book and milk testing plan exist, a selection scheme with all the above described steps can be found only for the Sarda breed.

The alternative closed nucleus scheme, with selection carried out in few flocks where advanced reproductive techniques are performed in order to accelerate the genetic gain (Nicholas and Smith, 1983; Rossi et al., 1995), does not seem to find practical application in dairy sheep with few exceptions, such as the case of the Comisana ewes in Sicily (Pinelli et al., 2002).

Enlargement of the genetic basis and new models for genetic evaluations

The modified version of the conventional scheme applied to dairy sheep has achieved some good results, but its problems are well known. The principal constraints can be identified in the insufficient genetic structure and in the limited size of the active population (involved in the milk performance testing scheme) in comparison to the remaining portion of the population (commercial population) that it is not involved in the milk performance testing scheme.

The active/commercial population (AP/CP) ratio in sheep is markedly lower than in dairy cattle, as can be observed in Figures 1a, 1b and 1c which report the AP/CP ratios for Italian dairy sheep breeds, French sheep breeds and Italian Holstein Friesian cattle, respectively.

Such a relevant difference can mainly be explained with the relative cost of dairy recording in sheep, at least three or four time higher than in cattle (Sanna and Casu, 1999). Moreover, the inclusion of milk chemical composition among the
breeding goals could result in a further marked increase in selection costs.

Simplified dairy recording schemes (Gonzalo et al., 2003) and techniques for the extension of incomplete lactations (Carta et al., 1998) have been developed in order to enlarge the number of controlled

Table 4. Some statistics of predictions obtained with the neural network methodology in Chios sheep (Kominakis et al., 2002).

| Plan 1 | Plan 2 | Plan 3 |
|--------|--------|--------|
| Parity |        |        |
| 3rd    | 4th    | 5th    |
| 3rd    | 4th    | 5th    |
| Mean AY (kg) | 198 | 198 | 198 |
| Mean PY (kg) | 196 | 199 | 198 |
| Correlation (AY, PY) | 0.87 | 0.89 | 0.94 |
| Pearson Rank Correlation (AY, PY) | 0.87 | 0.88 | 0.94 |
| Mean (AY-PY) | 2.2 | 0.8 | 0.1 |
| $\frac{\delta(AY-PY)}{AY} \times 100$ | 23.4 | 21.5 | 15.4 |

1 Actual yield; 2 Predicted yield.
Plan 1: Predicted yield estimated using 2 actual (out of 5) TD records plus 8 other input variables (country, herd, lactation number, lambing month litter size, controller, days in milk at first TD, lactation course) and 500 model vectors in the training phase;
Plan 2: Predicted yield estimated using 4 actual (out of 5) TD records, plus 10 others input variables (country, herd, lactation number, lambing month, litter size, controller, days in milk at first TD, lactation course after the second TD) and 1000 model vectors in the training phase;
Plan 3: Predicted yield calculated by using 4 actual (out of 5) TD records, plus 10 others input variables (country, herd, lactation number, lambing month, litter size, controller, days in milk at first TD, lactation course after the second, the third and the fourth TD) and 1000 model vectors in the training phase.
flocks. Regardless of their genetic merit, some referencing sires are used via laparoscopic insemination with frozen semen for successive years in different flocks to deliberately create genetic links, thus enabling genetic comparisons among cooperating flocks and years. Referencing sires actually have the dual role of creating genetic links among flocks and, once they are replaced by genetically superior rams, of producing more rapid dissemination of genetic gain (Simm, 2000). This strategy could be of interest for enhancing the effectiveness of selection and differentiating breeding goals in large breeds already subjected to selection. Moreover, it could be usefully used as a starting point for the improvement of small local breeds.

Genetic evaluation of dairy sheep is usually carried out by BLUP Animal Models methodologies having total lactation yield as dependent variable. In several dairy cattle populations, total lactation yield is being replaced by the direct modelling of test day measures (Schaeffer et al., 2000).

The main advantage of Test Day (TD) models - i.e. the direct correction of fixed effects, and especially of fixed effects whose impact changes over time (Swalve, 2000) - makes them particularly appealing for dairy sheep genetics. However, studies on TD models in dairy sheep deal essentially with the estimation of genetic parameters for milk production traits and somatic cell count (El Saied et al., 1998; Barillet et al., 2001b; Serrano et al., 2001, 2003) whereas their role as a real alternative to traditional BLUP Animal Models for current genetic evaluation tasks does not seem to be, at present, a real option. One of the causes can be found in the limited number of TD records per lactation available for dairy sheep, as a consequence of a shorter lactation length in comparison with dairy cattle, and in their distribution along the lactation. The effect of lactation length has been highlighted in a study carried out with a random regression model (i.e. the most updated version of TD models), on milk production data of Sfakia.

An alternative strategy for reducing the number of tests per lactation, and therefore increasing the number of controlled animals, could be the estimation of missing TD yields for the calculation of the total lactation yield by using forecasting models. With this aim in view, Time Series Analysis (Macciotta et al., 2000) and Neural Network techniques (Kominakis et al., 2002) have been proposed. Both methods are able to give accurate predictions (Table 3 and 4), even when the number of actual tests available is reduced by 30-40%, comparable with those achieved for dairy cattle with more complicated methods (Schaeffer and Jamrozik, 1996). These methods could represent an interesting option for enhancing the impact of breeding scheme on dairy sheep populations. Moreover, they should be easily implemented in a database at farm level as useful tools for management decisions.

The insufficient genetic structure of dairy sheep populations, i.e. the small size of half-sibs families and to the weak genetic connections among flocks, is a consequence of the low impact of artificial insemination (AI).

Several efforts are made to enlarge the quota of artificially inseminated animals by improving fertility rates of the traditional cervical insemination with fresh semen (about 45% in the Sarda breed), and by introducing new techniques such as the laparoscopic and the transcervical inseminations with frozen semen (Halbert et al., 1990).

A strategy in use for meat sheep breeds in the UK, known as the referencing sire scheme, could offer a tool for increasing genetic ties among flocks. Regardless of their genetic merit, some referencing sires are used via laparoscopic insemination with frozen semen for successive years in different flocks to deliberately create genetic links, thus enabling genetic comparisons among cooperating flocks and years. Referencing sires actually have the dual role of creating genetic links among flocks and, once they are replaced by genetically superior rams, of producing more rapid dissemination of genetic gain (Simm, 2000). This strategy could be of interest for enhancing the effectiveness of selection and differentiating breeding goals in large breeds already subjected to selection. Moreover, it could be usefully used as a starting point for the improvement of small local breeds.
sheep: fitting short lactation periods of around 140-150 days may not pose a substantial advantage to TD models in comparison with multitrait analysis, where each TD record is regarded as a different trait (Kominakis et al., 2001).

The application of random regression models, where the animal genetic effect is defined by using regression coefficients and allowing for covariances among them (Swalve, 2000; Schaeffer, 2004), requires additional care for dairy sheep, due to the high variability of lactation curve shapes (Figure 2). In the typical Mediterranean farming system, data recording usually starts from about 40 days in milk since the milk of the first month of lactation is suckled by the lamb. Therefore, the lactation peak, expected at around 3-4 weeks from lambing, is usually missed and the whole curve is has a downward trend. On the other hand, the favourable climatic and feeding conditions during spring usually cause a “false” lactation peak in the second half of the lactation (Figure 2). Such a situation could result in estimates of parameters of lactation curves that are out of the parameter space. A typical example is represented by the negative estimates of the b parameter of Wood incomplete gamma function (Wood, 1967) for curves that lack the lactation peak. A Bayesian iterative method, which based on the Wood function and combines the Gibbs sampler with the metropolis-Hasting algorithm to reject parameter out of the parameter space, has been proposed to solve this problem (Chang et al., 2001). Moreover, the use of Legendre orthogonal polynomials for which no prior knowledge about the lactation curve shape is required (Kominakis et al., 2001), has been suggested.

**The problem of genotype x environment interaction and the impact of low-input farming systems**

Selection programmes are essentially aimed at increasing farm profits by improving the genetic merit of animals for production traits. For dairy sheep, however, the relative importance of these traits may not be the same in all breeds or situations due to the great heterogeneity in production systems, environmental conditions and genetic level of animals.

Research carried out on Sarda sheep highlighted marked differences, both in the production levels and in the shape of lactation curve between ewes farmed in plain and mountain flocks, mainly due to differences in management, climate and pasture availability (Macciotta et al., 1999). Such heterogeneity could likely result in a relevant Genotype x Environment (G*E) interaction. The

Figure 2. Examples of different shapes of lactation pattern in sheep (● = normal; ---- = with a double peak; ____ = without peak) (Cappio-Borlino et al., 2002)
best genotype in a certain situation may be not the same in another, as the result of a different sensitivity of genes to environment or of the expression of different genetic pools. As a consequence, a trait measured in two different environments is to be regarded not as one trait but two (Falconer and Mackay, 1996).

Differences among breeding values (EBV) of rams estimated by using all lactations of the daughters available or only those obtained in flocks with low, medium or high production levels (average milk yield per lactation 152 kg, 193 kg and 232 kg, respectively) have been evidenced in the Sarda breed (Sanna et al., 2002). Correlations among EBV ranks are self-explanatory (Table 5), indicating that genotypes able to express best performances in high production level flocks were not the best in low producing flocks. Moreover, only three rams were in the top ten of all three ranks. This G*E interaction affects the efficiency of a breeding program, with problems in consistency of breeding value estimates and in the dissemination of the genetic progress in the commercial population.

There are two possible strategies to cope with the G*E problem. The first is aimed at selecting genotypes across all production conditions through a careful dissemination of semen of AI rams in all environments (Sanna et al., 2002). As a result, genotypes able to give the best average performance in all environments and more stable phenotypes can be obtained, even if the selection should be less effective in increasing the absolute genetic merit of animals. Moreover, statistical skills such as clustering techniques can be used to help in defining consistent contemporary groups in order to make the most appropriate comparisons (Powell and VanRaden, 2002). This is actually the choice of dairy cattle breeding in the USA and it seems the more realistic and easy to perform solution for dairy sheep.

The second approach starts from considering milk productions obtained in different environments as different traits. As a consequence, breeding goals should be diversified too. On the basis of the scheme depicted by Olesen et al. (2000), three typical scenarios of production for dairy sheep can be hypothesised (Table 6).

The first scenario deals with good farming conditions (flocks from plain areas, for example), where milk production traits represent the most suitable breeding goals. The need for reducing production costs should be pursued by improving the biological efficiency of the animal (i.e. functional trait, discussed later in the text). Moreover, the increasing consumer demand for foods that are safer and of high quality should be addressed by emphasizing milk quality traits.

Breeding strategies in marginal areas (flocks in mountain areas of Italy or in southern Mediterranean countries) should mainly be oriented to obtain genotypes that can give reasonable milk yields for the processing of typical products. Functional traits such as fertility, longevity, disease resistance, feeding efficiency, should be of primary importance. Moreover, an economically interesting option could be the improvement of meat production, by selecting for prolificacy (Barillet, 1997; Kominakis et al., 1997; Ligda et al., 2000; Pulina et al., 2001). In the more extreme situations, the use of local breeds should guarantee genotypes that best fit a particular environment and, at the same time, make an important contribution to the conservation of animal genetic diversity.

Finally, the growing relevance of organic livestock farming should be taken into account. In the last few years there has been an average annual increase of approximately 32% in the area farmed

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Table 5. Spearman’s correlations among genetic ranks obtained using different information (from Sanna et al. 2002).

|      | All | Low | Medium |
|------|-----|-----|--------|
| Low  | 0.79| 0.55| 0.42   |
| Medium | 0.75| 0.42| 0.45   |
| High | 0.63| 0.42| 0.45   |
This trend can represent a further cause for G*E interaction because a genotype well adapted to and performing well in a conventional farming system, might not do so in an organic one (Boelling et al., 2003). Such a low-input scenario, which may be of interest both for favourable and marginal areas, requires high management quality on behalf of the farmer and animals well adapted to the farming system. The improvement of functional traits and the exploitation of local breeds are consistent genetic strategies in these situations. In some European countries like Austria and Switzerland, work has begun on the development of “Ecological indexes” in cattle breeding, which includes not only production traits, but also functional traits (Boelling et al., 2003).

One of the main criticisms regarding the diversification of breeding goals, apart from the great difficulties for building and managing the breeding scheme, is based on the reduced income for flocks located in marginal areas and, in general, for low input systems that are less competitive in comparison to intensive production ones. However, a consistent comparison among different systems should be based not only on traits that have an actual market value (milk production and composition), but also on aspects whose importance cannot be quantified in monetary terms, but that are important for their social and ethical acceptation. Examples of these non-market traits are: the ethical values of improved animal welfare; reduced depletion of fossil energy and reduced environmental pollution obtained by improving the feeding efficiency of animals or their genetic resistance to diseases; the safeguard of environmental areas subjected to degradation hazards and the preservation of rare alleles linked to the exploitation of local breeds (Olesen et al., 2000). Governments should adequately support the genetic improvement of non-market-valued traits, indirectly resulting in an increase in income for farmers, by means of an appropriate policy (laws and prices).

Table 6. Some typical scenarios of production for dairy sheep and potential animal breeding strategies.

| Production circumstances | Priorities                                      | Breeding goals                                              |
|--------------------------|------------------------------------------------|------------------------------------------------------------|
| Intensive or semi-intensive flocks | Production                                      | Milk yield and quality                                     |
|                          | Reduction of costs                             | Feeding efficiency                                         |
| Improved environments    | Consumer safe                                  | Functional traits                                          |
| Good management level    | Animal welfare                                 |                                                            |
| Extensive farming systems| Typical products                               | Milk quality                                               |
| Use of marginal land     | Environmental protection                       | Meat yield                                                 |
| Heterogeneous environments| Socio-cultural aspects                        | Functional traits (capacity of adaptation, reproductive efficiency) |
| Low input systems        | Conservation of genetic diversity              |                                                            |
| Organic farming          | Low input system                               | Productive traits                                          |
|                          | Adaptations of animals                         | Functional traits                                          |
|                          | to different farming systems                   | Capacity of adaptation                                     |
|                          | Consumer safe                                  | of animals to low input                                    |
|                          | Maintenance of genetic diversity               | farming systems.                                           |

according to organic rules within the EU (Boelling et al., 2003).
New breeding goals: the evolution of milk quality concepts and the increasing importance of functional traits

**New breeding goals for milk quality**

The extension of dairy sheep breeding goals to milk quality and functional traits should be carefully evaluated. Aggregate genetic indexes that also consider milk fat and protein contents have been adopted in France for the Lacaune sheep, in order to prevent a possible reduction in milk fat and protein contents caused by the selection based on milk yield (Barillet, 1997). Since 1998, individual milk composition is routinely tested in the official testing scheme of the Sarda breed. As almost all sheep milk is processed into cheese, Othmane et al. (2002) suggested the use of individual cheese yield (ILCY) that can be recorded on each test day. This new variable, which is correlated to the milk fat and protein contents (0.52 and 0.38, respectively), has the advantage of expressing in a single term the suitability of milk for cheese processing. Obviously, the real economic advantage for implementation in a breeding scheme should be carefully evaluated.

On the other hand, it must be remembered that selection for milk quality has to deal with the continuous evolution of concept of quality, with a marked drift toward nutraceutical aspects. From this point of view, a significant example is represented by the recent great interest in milk fatty acid composition, particularly as far as the content of conjugated linoleic acid (CLA) isomers is concerned.

The term CLA indicates a mixture of positional and geometric isomers of octadecenoic acid with a conjugated double bond system. In vivo and in vitro studies report CLA's anticarcinogenic, antiatherogenic, antidiabetic, as well as antiobesity properties (Ip et al., 1991; Cook et al., 1993; Lee et al., 1994; Banni et al., 1996). Major natural sources of CLA are ruminant's milk and meat, especially from ewes (Juhreis et al., 1999). The cis-9, trans-11 CLA (rumenic acid) is the most frequent isomer in dairy products, representing from 75 up to 90% of the total CLA in milk fat (Secchiari et al., 2002). CLA isomers originate from the biohydrogenation processes of dietary linoleic acid carried out by rumen bacteria as Butyrivibrio fibrisolvens (Kepler et al., 1966). Another source of CLA in ruminants is the tissue synthesis of the rumenic acid (RA) via Δ9-desaturase of trans-11 octadecenoic acid (vaccenic acid), an intermediate metabolite of rumen biohydrogenation of linoleic and linolenic acids (Griinari et al., 2000). Although diet is the most important factor affecting milk fat CLA content (Bauman et al., 2001), differences in milk fat content of RA have been observed among individuals subjected to the same dietary regimen (Kelly et al., 1998; Secchiari et al., 2003). Since the majority of milk fat CLA is of endogenous origin, the activity of the Δ9-desaturase enzyme may be related to the observed variation among individuals (Griinari et al., 2000). Particularly, differences in the genomic region containing the Stearoyl Co-A (SCD) gene, which encodes for the Δ9-desaturase enzyme, may be supposed to affect the milk fat CLA content.

The SCD cDNAs of different species including hamster, rat, mouse, human and sheep (Ideta et al., 1998; Mihara et al., 1990; Ward et al., 1997) have been cloned. In mice, three isoforms (SCD1, SCD2, SCD3) have been identified on chromosome 19, whereas in rats only two isoforms were detected. In humans only a single functional SCD gene on chromosome 10 has been mapped. Like humans, ovines and bovines have only one SCD gene isoform identified (Ward et al., 1997; Chung et al., 2000), located on chromosome 22 and 26, respectively. Bovine and ovine SCD cDNA have been cloned, but reported sequences are probably incomplete (Ward et al., 1998; Chung et al., 2000). The genes isolated from mammalian species have a similar organisation with 6 exons and 5 introns, with the last exon containing the whole 3' UTR (untranslated region) characterised by several AUUUUA sequences, which have been proposed to influence the stability of SCD mRNA (Ntambi, 1999). Recently, Bernard et al. (2001) cloned goat SCD cDNA and reported both complete sequence and chromosomal localization. The total gene length is of approximately 15 kb. A genetic polymorphism has been identified in the caprine 3' UTR sequence: a trinucleotide (TGT) is present or absent. Given its position, a role in mRNA stabilisation was proposed for this polymorphism (Bernard et al., 2001).
Carta et al. (2003a) analysed milk fat CLA content and the CLA/vaccenic acid ratio in a backcross Lacaune x Sarda population. A remarkable variability in CLA content has been detected: individual variance accounted for 29.7% of the total phenotypic variance for CLA milk content and 34.4% for the ratio CLA/vaccenic acid, while sire variance resulted smaller (8.4% and 5.6%, respectively, for CLA milk content and the ratio CLA/vaccenic acid). Moreover, a QTL affecting the CLA/vaccenic ratio was found on OAR 22 (i.e. on the chromosome where the SCD gene is located). This result suggests a possible relationship between SCD gene polymorphism and its expression level, with a consequent effect on the quantity of CLA produced in the mammary gland from

Table 7. Some productive and functional traits for dairy sheep breeding (Barillet, 2001a).

| Trait                              | Model          | h²   | Breed     | Source          |
|------------------------------------|----------------|------|-----------|-----------------|
| Milk                               | Single trait   | 0.15 | Lacaune   | Barillet et al., 2001b |
| Milk                               | Single trait   | 0.04 | Manchega  | Serrano et al., 2003 |
| Milk                               | Multiple trait | 0.14 | Chios     | Ligda et al., 2002 |
| Milk                               | Single trait   | 0.12-0.13 | Lacaune | Rupp et al., 2003a |
| Meat (suckling lamb)               | Multiple trait | 0.04-0.12 | Lacaune | Barillet et al., 2001b |
| Milk yield efficiency              |                |      |           |                 |
| Reproduction                       |                |      |           |                 |
| Milking ability                    |                |      |           |                 |
| Health of mammary gland            |                |      |           |                 |
| Animal health                      |                |      |           |                 |

**Productive traits**

- Milk yield; protein content; fat content
- Prolificacy; maternal aptitude

**Functional traits**

- Milk yield; body weight; dry matter intake; body fat depots
- Sexual precocity; fertility
- Milking speed; mammary gland morphology
- Somatic cell count; mammary gland morphology
- Longevity, disease resistance, legs and foot conformation.

Table 8. Estimates of heritability for somatic milk cell score in some dairy sheep breeds.

| Trait | Model                | h²  | Breed     | Source          |
|-------|----------------------|-----|-----------|-----------------|
| LSCS  | Single trait         | 0.15| Lacaune   | Barillet et al., 2001b |
| LSCS  | Single trait         | 0.04| Manchega  | Serrano et al., 2003 |
| LSCS  | Multiple trait       | 0.14| Chios     | Ligda et al., 2002 |
| LSCS  | Single trait         | 0.12-0.13 | Lacaune | Rupp et al., 2003a |
| SCS   | Multiple trait       | 0.04-0.12 | Lacaune | Barillet et al., 2001b |
| SCS   | Repeatability TD     | 0.08| Lacaune   | Barillet et al., 2001b |
| SCS   | Repeatability TD     | 0.09| Churra    | El Saied et al., 1999 |
| SCS   | Repeatability TD     | 0.02| Manchega  | Serrano et al., 2003 |
| SCS   | Multiple trait       | 0.05-0.13 | Lacaune | Rupp et al., 2003a |

**LSCS** = Lactation mean of Somatic Cell Score computed as arithmetic mean of test day somatic cell score adjusted for days in milk

**SCS** = single test day somatic cell score
vaccenic acid. All the above-mentioned advance-
ments, even if not immediately applicable to the 
present situation of dairy sheep breeding schemes, 
open a very interesting scenario for the future 
implementation of molecular genetics in the selec-
tion of milk quality traits.

Functional traits

The economic efficiency of animal farming 
depends not only on revenues generated from the 
sale of products, but also on the magnitude of pro-
duction costs.

The term “functional traits” indicates a set of 
characteristics whose effect on the economic effi-
ciency of the animal is through reduction of costs 
rather than the increase in product output (Groen 
et al., 1997). Even if these traits are often difficult 
to record routinely and are characterised by low 
heritability values, their importance is now widely 
recognised by geneticists and members of dairy 
industry (Solkner and Fuerst, 2002). Some exam-
pies of both functional and productive traits are 
reported in Table 7.

Among functional traits, resistance to diseases 
has a great importance for livestock species. When 
conventional control measures such as vaccination 
or pharmacological therapies are either ineffec-
tive, unsustainable or uneconomic, the genetic 
approach can offer an interesting alternative 
(Raadsma et al., 1997). In fact, the existence of a 
genetic component in controlling susceptibility of 
animals to diseases has been shown for several 
pathologies even if the identification of a suitable 
measure for these traits remains a difficult task.

Resistance to mastitis represents a typical 
example of such a situation. With an estimated 
average prevalence of 20-30% (Bergonnier and 
Berthelot, 2003), mastitis is recognised as one of 
the most costly diseases of the dairy sheep indus-
try. The reduction of milk yield, alteration of milk 
composition and cheese-making properties, 
increased culling rate and veterinary expenses are 
its main economic consequences (Serrano et al., 
2003; Leitner et al., 2004). Nevertheless, direct 
measure of mastitis resistance is difficult in dairy 
sheep, due to the great prevalence of subclinical 
infections (about 95% of the cases) caused by coag-
ulase-negative staphylococci (Barillet et al., 2001b;
Rupp et al., 2002). On the other hand, an indirect 
selection against mastitis by using somatic cell 
count (SCC) as an indicator trait (Barillet et al., 
2001b) is constrained by several problems. The 
first is represented by the low values of heritability 
(Table 8) and by its large standard errors, also 
demonstrated in dairy cattle (Mrode and Swanson, 
2003; Haile-mariam et al., 2001), that raise doubts 
on the real usefulness of SCC as indicator of genet-
ic resistance to intramammary infections. 
Moreover, genetic parameter estimates are 
markedly affected by the kind of variable consid-
ered and by the statistical approach used (Table 
8). Finally, conflicting results exist in literature on 
genetic correlations between SCC and milk yield: 
some studies found unfavourable positive values 
ranging from 0.08 to 0.18 (Barillet et al., 2001b; 
Rupp et al., 2003a), indicating that as milk yield 
increases SCC also increases, whereas other stud-
ies found favourable negative genetic correlations 
from – 0.11 to – 0.16 (Ligda et al., 2002; Serrano et 
al., 2003). At present, only the Lacaune breeding 
program takes SCC into account.

An alternative approach could be the inclusion 
of SCC in an aggregate genotype that considers 
other functional traits related to milk production 
such as udder morphology, milking speed and per-
sistency of lactation. In particular, udder confor-
maition is a trait that greatly affects the number of 
manual interventions needed for extracting the 
milk retained in the udder (Casu et al., 2003).
Selection by milk yield has lead to increased cistern 
height and horizontal teats that impair machine 
milking ability (Serrano et al., 2002). A linear scale 
for the morphological appraisal of the udder has 
begun to be used in Italy and Spain (de la Fuente 
et al., 1996; Casu et al, 2002). Genetic parameter esti-
mates highlight a low to moderate genetic variabil-
ity for the trait (Table 9). Higher values found for 
the Sarda breed can be due to differences in the 
model used, particularly in the use of random con-
temporary groups, and in the size of the population 
analysed. Other measures, such as the size of the 
mammary cistern evaluated by ultrasound tech-
nique, can be considered (Nudda et al., 2000).

One of the most current issues in the E.U. is 
the improvement of genetic resistance to Scrappie, 
a disease in the group of transmissible spongiform
encephalopathies that includes the bovine (BSE) and the human (Creutzfeld-Jakob disease) variants. Scrapie is present in most European countries although with a rather low prevalence (Table 10). While the ethiology and the transmission mechanisms of the disease are not completely clear, a genetic component of the susceptibility to the disease has been demonstrated (Elsen et al., 1997; Secchiari and Manzo, 2001). The responsible gene is the Prion Protein locus (PrP) that encodes for the prionic protein, a neuronal cell surface glycoprotein that is present in animals affected by Scrapie in an abnormal isoform (PrP$^{sc}$) that accumulates in lymphoid tissues and in the central nervous system (Hurtado et al., 2002). Of the known 15 PrP alleles, five are most frequently found in dairy sheep populations (ARR, AHQ, ARH, ARQ, VRQ). Polymorphisms related to Scrapie susceptibility are those at codons 136, 154, 171 (Francois et al., 2002) (Table 11): the ARR allele is the most resistant whereas the VRQ allele is the most susceptible (Elsen et al., 1997; Francois et al., 2002). Frequencies of PrP alleles in different sheep breeds are reported in Table 12.

A selection programme aimed at improving Scrapie resistance started in France in 1995: during the 1995-2000 period AI rams VRQ carriers have been culled thus shifting the ARR frequency from 0.55 to 0.68 and from 0.15 to 0.39 in the Lacaune and Manech breeds, respectively (Barillet et al., 2002). Since 2002, young Lacaune rams candidates for progeny testing have been pre-selected on the basis of their PrP genotype.

Similar strategies will be soon applied in other dairy sheep breeds such as the Sarda and Chios breeds.

The inclusion of Scrapie resistance as a breeding goal in a selection scheme should not have neg-

| Trait                   | Sarda          | Manchega     |
|-------------------------|----------------|--------------|
| Teat placement          | 0.32-0.35      | 0.20         |
| Teat size               | 0.10           |              |
| Udder depth             | 0.24-0.25      | 0.19         |
| Udder attachment        | 0.25-0.29      | 0.06         |
| Udder shape             | 0.12           |              |
| Udder cleft             | 0.19           |              |

Table 10. Number of Scrapie cases in some EU countries.

| Period     | 1996-2000 | 2001 |
|------------|-----------|------|
| Italy      | 59        | 6    |
| France     | 50        | 34   |
| UK         | 500       | 280  |

Table 9. Heritability estimates for udder traits in Sarda (Casu et al., 2003) and Manchega (Serrano et al., 2002) ewes.
ative effects on the genetic improvement of milk production traits. Actually, no productive differences between ewes having a different Prp genotype have been detected in the Lacaune and Manech breeds (Barillet et al., 2002). These findings have been confirmed by Palhiere et al. (2003), who observed a regular increase in the total merit index (including milk yield, protein and fat content) of the Lacaune dairy breed during the 1995-2002 period (Figure 3). However, a reduction in the selection intensity in the male selection pathways, which account for the 80% of the genetic progress obtained in the Sarda breed (Carta and Ligios, 2003), is to be expected. In order to keep constant the number of young rams entering progeny testing, the number of potential candidates has to be increased, with a subsequent decrease in their average pedigree index whose magnitude depends on the frequency of the resistant allele in the population and on the selection pressure on the PrP genotype. The selection in favour of the resistant genotype, which implies the use of only ARR/ARR rams, would be highly effective in increasing the frequency of the resistant allele but would also have the greatest negative impact on the structure and on the efficiency of the breeding programme. On the other hand, the selection in favour of the resistant allele, which enables the use of rams that possess a single copy of the ARR, would be less efficient in selecting for Scrapie resistance but would have a less dramatic impact for the structure of the breeding scheme. Finally, eventual founder allele effects with an association between PrP genotypes and production traits should not represent a problem in breeds of large size like the Sarda.

**Table 11. Mutations of PrP gene related to sensibility levels to the Scrapie disease.**

| Codons | 136 | 154 | 171 |
|--------|-----|-----|-----|
| Aminoacids | Alanine (A) | Arginine (R) | Glutamine (Q) |
|         | Valine (V) | Histidine (H) | Arginine (R) | Histidine (H) |

**Table 12. PrP allele frequencies in some dairy sheep breeds.**

| Breed               | n. animals | ARR | ARQ | VRQ | AHQ | Source                   |
|---------------------|------------|-----|-----|-----|-----|--------------------------|
| Sarda               | 884        | 0.40| 0.51| 0   | 0.09| Carta and Ligios, 2003   |
| Valle del Belice    | 49         | 0.3 | 0.68| 0.01| 0   | Pernazza et al., 2003    |
| Massese             | 50         | 0.50| 0.45| 0.02| 0.03| Pernazza et al., 2003    |
| Comisana            | 50         | 0.41| 0.45| 0.10| 0.04| Pernazza et al., 2003    |
| Latxa               | 698        | 0.25| 0.71| 0.03| 0.004| Hurtado et al., 2002    |
| Lacaune             | 561        | 0.55| 0.43| 0.01| 0.01| Palhiere et al., 2003    |
| Manech Blond        | 315        | 0.17| 0.81| 0.02| 0.01| Palhiere et al., 2003    |
Perspectives of Marker Assisted Selection

The increased knowledge on genomic regions controlling quantitative traits of economic interest could be implemented into Marker Assisted Selection schemes for improving breeding value estimation, enhancing selection intensity and reducing generation interval (Cappio-Borlino et al., 1996; Russo and Fontanesi, 2001).

Researches of quantitative trait loci (QTLs) in almost all livestock species, and especially in dairy sheep, are constrained by the extensive time and resource requirements, mainly due to the large number of animals that have to be genotyped to obtain a reasonable statistical power of the experimental design (Rebai et al., 1995; Carta and Elsen, 1999).

Classical designs suggested for detecting QTLs in dairy cattle populations subjected to a conventional selection scheme, the daughter and the granddaughter designs (Weller et al., 1990), have been applied also to some dairy sheep breeds. Some QTLs affecting productive and functional traits have been detected (Table 13).

The power of daughter and granddaughter designs may be enhanced by means of selective genotyping (SG) and selective phenotyping (SP) techniques (Casu et al., 2003). In the SG only animals showing extreme phenotypes are genotyped at the marker loci. For example, in the case of milk yield, only ewes with the highest and lowest values of milk production should be included in the experimental design. This approach results in a reduction in the number of genotype analyses and, therefore, in research costs (Bovenhuis and Spelman, 2000).

When the trait of interest is difficult and expensive to record, the SP could represent a valid option. Individuals are first measured for a trait (TR1) that is easy and cheap to record and is correlated to the selection goal (TR2) (for example, SCC and genetic resistance to mastitis). Then the TR2 is recorded only on individuals showing extreme TR1 phenotypes (Medugorac and Soller, 2001).

However, positional cloning of QTLs remains elusive and time consuming, mainly because in a typical genome scan QTLS are mapped within a 20 cM interval. This means that it is likely that hundreds of genes are within the confidence limits

Figure 3. Joint evolution of ARR allele frequency and total merit index in the Lacaune dairy breed (Palhiere et al., 2003).
of the QTL making the identification of the desired gene difficult \cite{Mc Rae et al., 2002}. A dense QTL map could be obtained by using linkage disequilibrium techniques that have been largely applied to human genetic studies. Rather than follow the segregation of marker alleles among related individuals of a known phenotype, linkage disequilibrium mapping tests for associations between marker alleles (or marker haplotypes) and traits value and can be applied to large samples of unrelated individuals \cite{Mc Rae et al., 2002}.

Conclusions

As a general conclusion, it can be said that dairy sheep breeding tends to follow the general framework developed for dairy cattle. Fundamental steps are the improvement of genetic models used to estimate breeding values, a progressive extension of breeding goals to functional and milk quality traits, an integration between quantitative and molecular genetics. Also new market solutions, such as the single breed cheese, may represent an interesting approach in order to contribute to preserve autochthonous breeds, similar to what is done with dairy cattle. However, in comparison with dairy cattle, the process is clearly slower and more difficult due to the peculiar characteristics of this species, to its farming system, to its lower economic importance and to the limited international interest in dairy sheep industry.

Actually, genetic progress obtained by conventional breeding schemes is appraisable but limited to few breeds and only to milk yield. Considering the magnitude of economic resources needed to organise and manage such schemes and their great technical, economical and social complexity, an increase in the number of sheep breeds involved in effective selection programmes does not seem to be a realistic future option. On the other hand, studies on G*E interaction have clearly demonstrated that efforts aimed at producing animals of high genetic merit can be fruitless as a result of scarce management and adverse environmental conditions.

The extension of breeding goals to milk composition traits, including also milk quality traits, could be justified only for breeds of economic importance and characterised by a marked integration of the different sectors of the dairy industry (production, processing and marketing).

\begin{table}
\centering
\begin{tabular}{|l|l|l|l|}
\hline
Trait & Location & Breed & Source \\
\hline
CLA/Vaccenic acid ratio in milk fat & OAR22 & Sarda*Lacaune BC & Carta et al., 2003 \\
Milk fat content & OAR20 & Sarda*Lacaune BC & Carta et al., 2003 \\
Milk protein content & OAR6 & Churra & Diez-Tascon et al., 2001 \\
Milk protein content & OAR1 & Sarda*Lacaune BC & Carta et al., 2003 \\
Milk yield & OAR3 & Sarda*Lacaune BC & Carta et al., 2003 \\
Resistance to Nematodes & OAR3 & Sarda*Lacaune BC & Scala et al., 2002 \\
Somatic Cell Score & OAR6 & Sarda*Lacaune BC, Lacaune & Rupp et al., 2003b \\
Teat placement & OAR9, OAR14 & Sarda*Lacaune BC & Casu et al., 2003 \\
Udder attachment & OAR12 & Sarda*Lacaune BC & Casu et al., 2003 \\
\hline
\end{tabular}
\caption{Results on researches on QTLs in dairy sheep breeds.}
\end{table}
The impact of molecular genetics is, at present, limited to the genetic control of diseases but it could represent an interesting option, especially for functional traits that in dairy sheep are more difficult and costly to record than in dairy cattle.

As far as future perspectives are concerned, the main guidelines of international agricultural policy should be taken into account. Relevant points are: food safety, conservation of genetic diversity, safeguard of the environment, animal welfare, improvement of social conditions for farmers. Efforts for developing alternatives based on a reduced level of investments, a more active role of farmers (direct test recording by the owner, for example), and on the exploitation of local breeds should be made.

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