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ABSTRACT

The aim of the present work was to estimate genetic variability in Chianina (CH), Marchigiana (MC) and Romagnola (RO) breeds using pedigree information. Different approaches based on probability of identity-by-descent (effective population size through an increase in inbreeding N_e) or probability of gene origin (total number of founders f, effective number of founders f_e, ancestors f_a and founder genomes f_g) were used. Reference populations were defined using female animals born between 1996 and 2000 where both parents are known. Generation intervals were 5.35, 4.93 and 5.15 years for CH, MC and RO, respectively. The total number of founders were 7092, 11947, 3928, for CH, MC and RO, respectively. Complete generation equivalent showed the relative high quality of pedigree information: 5.66 for CH, 4.54 for MC and 4.95 for RO. For CH, MC and RO, respectively, a f_e value of 152.1, 70.9 and 89.8, a f_a value of 73.6, 48.0 and 59.5 and a f_g value of 39.5, 25.0 and 38.5, were calculated. When inbreeding was used effective population sizes were 138, 122 and 124 for CH, MC and RO, respectively.

Parameters derived from the probabilities of gene origin were variable among the investigated breeds and the results for MC demonstrate the need to pay specific attention to breeding strategies.

Key words: Pedigree analysis, Italian beef cattle, Genetic diversity, Probabilities of gene origin.

RIASSUNTO
VARIABILITÀ GENETICA DI TRE RAZZE BIANCHE ITALIANE DA CARNE BASATA SULLE INFORMAZIONI DA PEDIGREE

Scopo del presente lavoro è stato stimare la variabilità genetica delle razze bovine da carne Chianina (CH), Marchigiana (MC) e Romagnola (RO) usando le informazioni derivanti dai pedigree. Sono stati utilizzati due differenti metodi il primo basato sulla probabilità di identità per discendenza mendeliana (numero effettivo di popolazione stimato attraverso l'aumento di consanguineità N_e) ed il secondo sulla probabilità di origine genica (numero totale di fondatori f, numero effettivo di fondatori f_e, ancestrali f_a e numero rimanente genomi fondatori f_g). La popolazione di riferimento è stata definita come tutti i soggetti femmina nati tra il 1996 ed il 2000 con i due genitori conosciuti. L'intervallo medio di generazione è risultato di 5,35, 4,93 e 5,15 anni per CH, MC e RO, rispettivamente. Il numero totale dei fondatori è risultato essere di 7092, 11947, 3928, per le tre razze nell'ordine, CH, MC e RO. Il valore delle generazioni equivalenti complete evidenzia una buona qualità delle informazioni da pedigree: 5,66 generazioni per CH, 4,54 per MC e 4,95 per RO. Il numero effettivo di fondatori ha presentato valori di 152,1, 70,9 e 89,8, per CH, MC e RO mentre il numero effettivo di ancestrali ed il numero rimanente di genomi fondatori sono stati pari a 73,6, 48,0 e 59,5 ed a 39,5, 25,0 e 38,5, rispettivamente per CH, MC e RO. La dimensione effettiva di popolazione stimata attraverso l'aumento di consanguineità è stato pari a 138, 122 e 124 per CH, MC e RO, rispettivamente. I parametri derivanti dalle probabilità di origine genica sono risultati differenti tra le razze studiate ed in particola modo per la razza Marchigiana sembra necessaria una specifica attenzione nelle strategie selettive.

Parole chiave: *Analisi pedigree, Razze bovine italiane da carne, Diversità genetica, Probabilità di origine genica.*

Introduction

Maintaining genetic diversity is one of the goals in livestock management and knowledge of this diversity is the basis for effective selection and conservation programmes. Populations of limited effective size are strictly dependent on the maintenance of such genetic diversity, but this is also true of breeds where a limited number of sires are intensively used (Nomura *et al.*, 2001) or in larger populations which have a limited exchange of animals (Zechner *et al.*, 2002).

The trend in inbreeding is widely used to quantify the rate of genetic drift in a population, but in domestic animals the efficiency of this approach may be limited, as extensively reviewed by Boichard *et al.* (1997). An alternative approach is to analyse the probabilities of gene origin; for this method, the genetic contributions of the founders of the current population are measured. These founder contributions could be combined to derive the 'founder equivalents', as proposed by Lacy (1989). In addition, Boichard *et al.* (1997) adapted the method to account for the bottlenecks in the pedigree, deriving an effective number of ancestors. These parameters are useful when analysing the consequences of selection in small populations.

European dairy cattle breeds were thoroughly investigated from this point of view (Maignel *et al.*, 1996; Sölkner *et al.*, 1998; Roughsedge *et al.*, 1999; Baumung and Sölkner, 2002; Maltecca *et al.*, 2002) however, by comparison there are few studies concerning genetic variability in beef cattle breeds (Boichard *et al.*, 1997; Gutiérrez *et al.*, 2003).

The current study is intended as an investigation of three Italian beef cattle breeds in which genetic evaluation for growth and meat quality using BLUP animal model methodology has been underway since 1996 and the resultant drastic changes in breeding policy may have caused a reduction in genetic variability.

The aim of the work presented here was to estimate genetic variability in Chianina, Marchigiana and Romagnola beef cattle breeds using both probability of identity-by-descent and probability of gene origin approaches.

Material and methods

Data and pedigree information

Data used in the present paper came from Chianina, Marchigiana and Romagnola beef cattle breeds with 260,441, 350,710 and 119,489 animals, respectively (Table 1). For each animal included in the matrix relationship the following information was available: sire, dam, date of birth, sex, province and herd. Data were used to compute:

- animals in the reference population;
- average number of ancestors;
- maximum number of generations traced;
- complete generation equivalent defined as the sum of the proportion of known ancestors over all generations traced;
- percentage of known ancestors at each generation;
- average generation interval defined as the average age of parents when their progeny are born, that is to say, upon becoming parents themselves.

Genetic variability parameters

Inbreeding was computed according to the method proposed by Meuwissen and Luo (1992) and the effective size through an increase in inbreeding (N_e) was derived from the trend in inbreeding for the last generation. Effective population size was also estimated according to the method proposed by Lande and Barrowclough (1987), which takes into account the variance in progeny number (N_{el}).

The measures based on probabilities of gene origin (Boichard, 2002) investigated in this study were the total number of founders (f); the effective number of founders (f_e), i.e. the number of equally contributing founders that could be expected to produce the same genetic diversity as that which exists in the population under study; the effective number of ancestors (f_a) where the marginal contribution of each ancestor (i.e. the contribution not yet explained by the other ancestors) should be considered; the effective number of founder genomes (f_g) analysing the probability that a given gene present in the founders (i.e. a 'founder gene') is still present in the population under study. The effective number of founder genomes was comput-

Table 1.   Pedigree information available for the three breeds

		Chianina	Marchigiana	Romagnola
Animals in the pedigree file	n.	260,441	350,710	119,489
Animals in the reference population	''	2488	2606	1079
Average n. of ancestors		224	107	126
Complete generation equivalent		5.66	4.54	4.95
Maximum n. of generations traced		14	12	13
% of known ancestors at generation:				
2		92.69	85.23	97.09
4		84.81	71.43	80.83
6		61.95	39.72	37.25
8		16.39	4.66	6.72
10		1.20	0.10	0.41

ed following the algorithm described by Boichard *et al*. (1997).

For the analyses, the reference populations were defined as those female animals born between 1996 and 2000 where both parents are known.

Results and discussion

Table 1 provides information about the pedigree data available for all three breeds. The average number of ancestors (Table 1) is quite high for all three breeds and greater than that found in French dairy breeds (Maignel *et al*., 1996); the number of complete generation-equivalent (i.e. the number of generations in a comparable complete pedigree) exceeds the value of 4.5 which is greater than the value found for the Montbéliarde breed and not so far from that found for the French Holstein breed (Maignel *et al*., 1996) which reached a value of 4.75. Despite a higher number of animals in the pedigree file Marchigiana cattle seems to be the smallest population from a genetic point of view.

Among the breeds under study, Chianina shows more accurate pedigree information. Nevertheless, its pedigree should be considered as incomplete because only 62 % and 16.4 % of ances-

tors were known at best for generations 6 and 8, respectively. Similar results were found by Boichard *et al*. (1997) when they investigated French cattle population, whereas Baumung and Sölkner (2002) and Sölkner *et al*. (1998), while investigating Austrian cattle breeds, related values lower than those found in the present paper.

Table 2 reports the average generation interval for the three breeds calculated considering only the reproducing progeny. The estimates ranged from 4.36 to 6.02 with little difference among breeds and pathways. As expected the two sires-offspring pathways showed shorter generation intervals and this is probably due to the early replacement of the sires when artificial insemination is used, as already reported by Gutiérrez *et al*. (2003). The longest generation interval corresponds to the second largest population, whereas the largest population, i.e. Marchigiana, shows the shortest generation interval perhaps due to the breeding policy of quick replacement of animals for this breed which is characterised by small herds with intensive management.

Table 3 presents the various measures of genetic variability. The average inbreeding coefficient was around 2% for all the three breeds. The effective sizes (N_{el}) based on the method proposed by Lande and Barrowclough (1987) were 27.83,

Table 2.   Generation intervals (years) for the three breeds calculated on reproducing progeny.

	Chianina	Marchigiana	Romagnola
Sire/Son	4.44	4.36	4.80
Sire/Daughter	4.84	4.62	5.09
Dam/Son	6.02	5.27	5.44
Dam/Daughter	5.92	5.47	5.28
Averaged	5.35	4.93	5.15

Table 3.   Results of the pedigree analysis for the reference populations.

	Chianina	Marchigiana	Romagnola
Average inbreeding coefficient	0.0206	0.0215	0.0188
Inbreeding increase[a]	0.0036	0.0041	0.0040
Effective size (N_{el})	27.83	7.51	29.99
Effective population size (N_e)	138	122	124
Total n. of founders (f)	7092	11947	3928
Effective n. of founders (f_e)	152.10	70.90	89.80
Effective n. of ancestors (f_a)	73.61	48.02	59.55
Effective n. of founder genomes (f_g)	39.46	25.05	38.46

[a] *During the last generation*

7.51 and 29.99, for CH, MC and RO, respectively. These results are quite low but the measure could be strongly influenced by the number of individuals in an initial bottleneck, as reported Lande and Barrowclough (1987). The effective population sizes through an increase in inbreeding (N_e) for CH, MC and RO were 138, 122 and 124, respectively. These values are in agreement with those found in Austrian (Baumung *et al.*, 2002) and Spanish (Gutierrez *et al.*, 2003) beef cattle populations. Figure 1 reports the inbreeding trend for the three breeds; a steady increase could be observed and the inbreeding coefficient reaches values of 2%, similar to those found for other European cattle breeds (Sölkner *et al.*, 1998; Baumung and Sölkner, 2002; Gutierrez *et al.*, 2003).

These results are difficult to interpret, because they depend heavily on the completeness of pedigree information whereas the parameters derived from the probabilities of gene origin are less sensitive to the pedigree completeness (Boichard *et al.*, 1997).

The criteria derived from the probabilities of gene origin provided low results confirming that the Marchigiana breed is the smallest of the three populations studied. This implies that the contributions of founders were more unbalanced than in the other two breeds; whereas, for the smallest population in absolute size, i.e. the Romagnola breed, the adoption of different breeding policies could have lead to a better equilibrium in the population; artificial insemination is less widespread

Figure 1.   Inbreeding trend for the three breeds.

Table 4.   Description of the most important ancestors.

	Chianina	Marchigiana	Romagnola
Proportion of genes contributed by (%):			
First ancestor	5.89	8.83	6.38
First 10 ancestors	31.16	36.30	33.72
First 20 ancestors	40.92	49.09	46.10
First 50 ancestors	54.84	62.44	61.05
N. of ancestors contributing:			
50 % of the pool	37	21	25
80 % of the pool	447	926	236

in the Romagnola breed with extensive use of natural service bulls.

The lower value of f_e in comparison to the total number of founders (f) implies an unbalanced use of founders for all three investigated breeds.

As expected, the values for f_g were always lower than those for f_a which considers only the genetic variability of the founders and the bottlenecks, whereas, f_g also considers the random loss of alleles during segregation.

Table 4 gives the proportion of genes contributed to the reference population by the most important ancestors. For the Marchigiana breed the most important ancestor contributed almost 9% of the genes in the reference population whereas for Chianina and Romagnola breeds this contribution was around 6%. Actually, very few ancestors contribute the major part of the gene pool for the

Table 5. Proportion of genes (%) in the population from the five most important ancestors for the three breeds.

Most important ancestors	Sex	Year of birth	Frequency
Chianina:			
Orizio	M	1976	5.89
Zuvello	M	1983	4.93
Bando	M	1966	4.40
Esco	M	1988	2.87
Tempo	M	1980	2.61
Marchigiana:			
Mirino	M	1990	8.83
Soio	M	1976	7.13
Condono	M	1983	3.66
Damasco	M	1994	3.26
Mucco	M	1971	2.57
Romagnola:			
Ramses	M	1975	6.38
Dritto	M	1964	5.39
Telamone	M	1969	4.86
Titano	M	1969	4.41
Fiasco	M	1966	3.08

breeds under investigation. The first 20 ancestors explain more than 40% of the gene pool and the marginal contribution of the first 50 ancestors reaches values around 60%.

Marchigiana seems to be the less diverse population, genetically speaking, among the breeds considered. Nevertheless, the values found for this breed are similar to those found in other studies (Maignel *et al.*, 1996; Sölkner *et al.*, 1998; Gutierrez *et al.*, 2003; Vozzi *et al.*, 2004) on several cattle breeds confirming the overall positive situation for the Italian beef cattle breeds in terms of genetic variability. Furthermore, it must be pointed out that the number of founders accounting for 50% of population genes ranges from 21 to 37 which implies an intense use of certain founders through their descendants as also reported by Gutiérrez *et al.* (2003) for Spanish beef cattle breeds. The most important female ancestors were

ranked 7 in Chianina, 12 in Marchigiana and 6 in Romagnola with marginal contributions of 2.2%, 1.6% and 2.1%, respectively. Of the first 100 most important ancestors, 33, 44 and 47 were females for Chianina, Marchigiana and Romagnola, correspondingly.

In Table 5, the five most important ancestors for each breed are shown. In Romagnola, the most important ancestors date back to the sixties confirming a homogeneous use of several bulls. In Marchigiana, the situation is completely different; the most dominant bull dates back to 1990 and another two bulls out of the top five were born after 1980. The intense use of a few bulls in the recent past could lead to a high increase in inbreeding in the future unless appropriate policies for inbreeding control are applied.

Estimates for the parameters of gene origin for some European cattle breeds are presented in

Table 6.   Estimates of parameters of probability of gene origin for some European cattle breeds.

Breed	Reference population	Total number of founders (f)	Effective number of founders (f_e)	Effective number of ancestors (f_a)	Effective number of founder genomes (f_g)
Chianina[a]	2488	7092	152	74	39
Marchigiana[a]	2606	11947	71	48	25
Romagnola[a]	1079	3928	90	59	38
Abondance[b]	9971	6109	69	25	17
Normande[b]	301402	138291	132	40	22
Limousine[b]	93591	26656	790	360	206
Brown Swiss[c]	13856	6291	84	28	19
Montbéliarde[c]	331600	122981	146	63	36
Tarentaise[c]	5817	2942	50	17	15
Holstein[c]	2316371	802289	140	43	30
Simmental[d]	293198	85201	221	114	94
Braunvieh[d]	90484	29465	97	52	41
Pinzgauer[d]	19644	10244	113	39	21
Tux-Zillertal[e]	471	112	21	14	10
Carinthian Blond[e]	230	305	30	29	23
Alistana[f]	513	1207	265	56	-
Asturiana de los Valles[f]	16509	10107	846	163	-
Pirenaica[f]	8604	3279	153	58	-
Morucha[f]	1193	990	130	105	-
Avileña – Negro Iberica[f]	13034	4301	68	59	-

[a] present study; [b] Boichard et al. (1997); [c] Maignel et al. (1996); [d] Sölkner et al. (1998); [e] Baumung and Sölkner (2002); [f] Gutiérrez et al. (2003).

Table 6. As expected, the reference population size is rather different among breeds. Dairy cattle breeds showed higher values in terms of total number of founders, whereas the situation is completely different when observing the three criteria f_e, f_a and f_g. The results for the effective number of ancestors (f_a), which accounts for selection rate, family size and bottlenecks in pedigree, were lower for dairy breeds irrespective of effective population size. The strong difference between f_e and f_a for dairy breeds is perhaps related to their breeding policies with a high rate of artificial insemination and short-term oriented selection procedures, whereas beef cattle breeds showed higher values of f_a even when the reference population was small, as in the case of Asturiana de los Valles and

Morucha (Gutiérrez *et al.*, 2003). When looking at the breeds studied for this work, the f_a parameter is relatively good for Chianina while on the other hand it is very small in the Marchigiana breed and it did not reach the minimum value recommended to prevent the loss of genetic variability (Meuwissen, 1999).

These results, as mentioned before, are undoubtedly related to the breeding policies adopted in these populations and studies to identify the more frequently used blood lines, such as those proposed for the swine population (Toro *et al.*, 2000), could be useful tools to re-equilibrate the effective population size.

It is well known that selection of animals based on pedigree information and the BLUP animal model evaluation concentrates gene origins on just a few families. However, the introduction of some modifications for existing selection programmes may lead to genetic improvement, maintaining or improving genetic variability in the midterm.

For instance selection based on carcass weight and/or carcass yield instead of on growth rate could allow the inclusion of some bulls or bloodlines previously less considered. Similar results may also be obtained by adding new criteria to selection indexes, such as functional longevity, the importance of which has been recently investigated in the Chianina breed (Forabosco *et al.*, 2004, 2005). The use of a new parameter, such as average relatedness (Dunner *et al.*, 1998), could be very interesting if it was used for monitoring genetic variability. Average relatedness provides information both for description and management purposes and the coefficient computed for each individual can be used for mating purposes and also to equalize the relative genetic representation of different bloodlines in relation to the population.

Nevertheless, as suggested by Gutierrez *et al.* (2003), appropriate monitoring for genetic variability requires commitment in pedigree recording in order to reduce the information gaps along the pedigrees in an effort to achieve a better knowledge of genealogy.

Conclusions

Probability of gene origin can be considered a very useful tool for describing the structure of a population after a small number of generations and, in the presence of incomplete pedigree information, it has led to better estimates of effective size when compared with the method of probability of identity-by-descent.

The genetic status of the three populations under discussion is somewhat different but unequal founder contributions could be shown in all populations. The main conclusion of this study is that the Marchigiana beef cattle breed is the smallest population in terms of genetic variability and this could be related to heavy usage of some AI bulls, population size and the selection of few bull sires. The other two populations, the Chianina and the Romagnola breeds, have a greater effective size from the genetic point of view.

Making some simple modifications to current selection programmes might enlarge the gene pool by including bull sires not previously considered. Such modifications could lead to an increase in genetic diversity and the maintenance of genetic variability in the mid to long term. In this context the parameters derived from probability of gene origin could help in the analysis of the consequences of selection choice and in the prediction of genetic variability evolution.

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