Original article

Genetic variability of six French meat sheep breeds in relation to their genetic management

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Abstract – Some demographic parameters, the genetic structure and the evolution of the genetic variability of six French meat sheep breeds were analysed in relation with their management. Four of these breeds are submitted to more or less intense selection: the Berrichon du Cher (BCH), Blanc du Massif Central (BMC), Charollais (CHA) and Limousin (LIM); the other two breeds are under conservation: the Roussin de La Hague (RLH) and Solognot (SOL). Genealogical data of the recorded animals born from 1970 to 2000 and of their known ancestors were used. The most balanced contributions of the different flocks to the sire-daughter path was found in the SOL. In the BCH, a single flock provided 43% of the sire-AI sire path, whereas the contributions of the flocks were more balanced in the BMC and LIM (the only other breeds where AI is used to a substantial amount). The distribution of the expected genetic contribution of the founder animals was found to be unbalanced, especially in the BCH and LIM. The effective numbers of ancestors (founders or not) for the ewes born from 1996 to 2000 were equal to 35 (BCH), 144 (BMC), 112 (CHA), 69 (LIM), 40 (RLH) and 49 (SOL). Inbreeding was not analysed in the BMC, due to incomplete pedigree information. From 1980 on, the rates of inbreeding, in percentage points per year, were +0.112 (BCH), +0.045 (CHA), +0.036 (LIM), +0.098 (RLH) and +0.062 (SOL). The implications of the observed trends on genetic variability are discussed in relation to the genetic management of each breed. The need for a larger selection

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basis in the BCH, the efficiency of the rules applied in the SOL to preserve the genetic variability and the need for a more collective organisation in the CHA and RLH are outlined.

genetic variability / inbreeding / selection schemes / conservation programmes / sheep

1. INTRODUCTION

The preservation of genetic variability within selected populations has received increasing attention over recent years (see for example, [27]). It has been shown that when selection occurs, the relationship between reproducing animals and the inbreeding within their progeny are higher than under pure genetic drift [8,20]. Different methods have been proposed to combine immediate genetic gain and preservation of the genetic variability, *e.g.* by using the optimal contributions of parents for both a maximum genetic gain and a targeted increase of inbreeding [12], or by putting less emphasis on family information in the selection index [26]. In conservation programmes for endangered breeds, little or no attention is paid to genetic gain, and restraining the rate of inbreeding is the main goal. Some more or less complex methods have been proposed for that purpose [22]. Considering both selection and conservation, some simple demographic parameters have a large impact on the evolution of the genetic variability and largely depend on both the biology of the species and the management of the population: numbers of male and female parents, (dis)equilibrium of progeny sizes and length of reproductive life.

Genetic analyses using pedigree information have been extensively used to assess the genetic structure of livestock populations. Some examples of such analyses, considering a number of breeds of more or less large extent, may be given in horses [13], dairy [10,14,24] and beef [5,18] cattle, dairy sheep [15] and pigs [9]. On the contrary, studies with meat sheep have considered one or two breeds only, which are either endangered or which had been subjected to little selection [3,6,19]. The purpose of this work was to investigate the genetic structure of some French meat sheep breeds, using genealogical data, and to compare the evolution of their genetic variability in the context of their management practices. Both selected and endangered breeds, representing a large range of situations, were considered.

2. POPULATIONS STUDIED AND AVAILABLE DATA

2.1. Populations studied and their management

In 2000, the total number of ewes in France was 6.6 million, which comprised 5.2 million (79%) suckling ewes and 1.4 million (21%) milking ewes [23]. These ewes represent 60 different pure breeds and different crosses.

For this study, it was not possible to consider all these populations: six pure breeds, representing a large range of management situations, were considered (Tab. I). Three of these breeds, the Blanc du Massif Central, Limousin and Solognot, are kept in areas with harsh environmental conditions, and both robustness and good maternal abilities are their main characteristics. The other three breeds are kept in more favourable areas. Two of them, the Berrichon du Cher and Charollais, are specialised in growth and carcass traits and are widely used for terminal crossing. More details about these breeds are available on http://www.brg.prd.fr/brg/ecrans/animalesBd.htm or http://www.inapg.fr/dsa/especes.

Four of the breeds considered here have a selection programme, including on-farm performance recording, individual testing of rams in station, and progeny testing of rams (Tab. I). The Blanc du Massif Central is one of the sheep breeds in France with the highest population size and has large and stable number of recorded or tested animals. Due to the extensive use of pastures by flocks with a large number of ewes and several rams, the identity of the sire is often unknown in this breed. However, the young Blanc du Massif Central rams to be tested always have a known sire. The other three breeds have a smaller number of recorded ewes, especially the Berrichon du Cher, and a smaller number of tested rams. The Charollais has stable numbers of recorded ewes but a very low performance recording rate (4% over the total ewes). The number of Limousin and Berrichon du Cher recorded ewes has decreased in the last ten years. For breeders with performance recording, according to breeders' associations rules, providing young suckled rams for individual testing in station is a voluntary initiative in the Berrichon du Cher and Charollais, whereas it is mandatory for the Blanc du Massif Central and Limousin breeds. Except in the Charollais, the majority of young rams entering the testing station have an Artificial Insemination (AI) sire: 62% in the Blanc du Massif Central, 81% in the Berrichon du Cher and 96% in the Limousin. The young rams to be progeny tested are selected on the basis of their individual tests. After progeny testing, the best sires are used mainly for AI, with the exception of the Charollais, with AI being little used by its breeders. This little use of AI in the Charollais may be partly explained by the small average size of the flocks.

The other two breeds have a smaller population size. Their breeders have developed a conservation programme, and selection is mainly within-flock. These two breeds, however, show different pictures. The Solognot was the first breed of farm animals in France to develop a conservation programme in 1969, but is still considered to be endangered. In order to restrain genetic drift, a genetic programme was developed in 1976, based on three rules: (i) using as many rams as possible and avoiding a too large progeny size for a given ram; (ii) quickly replacing old rams with young ones; and (iii) splitting the breed

Table I. Some characteristics of the six sheep breeds studied and of their data files.

Kind of programme		Selection				Conservation	
Breed	Full name	Berrichon du Cher	Blanc du Massif Central	Charollais	Limousin	Roussin de La Hague	Solognot
	Abbreviation used in this paper	BCH	BMC	CHA	LIM	RLH	SOL
General census (2000)	Total number of ewes	37 000	359 000	282 000	38 000	22 000	2500
On farm performance recording (2000)	Number of recorded ewes	3132	38 800	11 445	12 756	1191	603
	Number of recorded flocks	28	111	152	54	29	12
	Average number of ewes per flock	112	350	75	236	41	50
Flock-book (2000)	Number of registered flocks	23	83	143	51	26	12
Annual number of rams tested	Individual test in station: growth rate	120	750	220	145	–	–
	Progeny testing in station: carcass traits	10	22	10	–	–	–
	Progeny testing on farm: maternal qualities	–	22	–	10	–	–
Content of data files	Total number of animals	31 596	215 224	77 377	67 788	9812	5063
	Total number of flocks	257	873	1183	664	237	122
	Total number of sires	1892	2631	5732	2136	556	381
	Number of ewes born in 1996–2000 with both parents know (female reference population)	3984	18 699	14 599	10 108	1335	567

into 12 reproduction groups and managing mating according to this structure. The first rule simply comes from the analytical expression of a theoretical effective population size (see [7], for example). The second rule comes from theoretical considerations on the effective population size with overlapping generations [7] and its value has been confirmed by simulation studies on the rate of inbreeding without selection in sheep and goats [21] or cattle [4] populations. The third rule corresponds to the so-called "rotational scheme"; for a detailed description of this method and for results about its value for minimising the rate of inbreeding, see [4, 21]. In order to facilitate the supply and exchange of rams between Solognot flocks, a collective rearing station was built in 1982. Each year, after suckling, young rams are kept in this station and, when they are sexually mature, they are sold to the breeders. The selection within the station is weak: only a few rams with individual defects are not sold for reproduction. The Roussin de La Hague breed has a substantialy larger population size than the Solognot breed (Tab. I). However, during the early 1980's, the total number of Roussin de La Hague ewes was around 8000 and the breed was considered to be endangered. No collective management of rams has been developed for this breed and the exchanges of animals between flocks are based on individual breeders' decisions.

2.2. Data

The national file for genetic evaluation was used, including all recorded animals born from 1970 to 2000 and their known ancestors (Tab. I). Coefficients of inbreeding were computed for all animals in the data file and the evolution of inbreeding over time was assessed by grouping animals per birth year (see next). On the contrary, some analyses were of interest mainly or only for the most recent cohorts of animals. Especially, the analysis of probabilities of gene origin was performed on ewes born from 1996 to 2000 and with both parents known; this group was called the female reference population (Tab. I).

3. METHODS

All analyses were performed for each breed separately. The demographic analysis was intended to reveal some consequences of the genetic management of each breed and to contribute to the understanding of genetic results. The genetic analysis, from pedigree information, focused on probabilities of gene origin, on the one hand, and on inbreeding and relationship (according to Malécot [11]), on the other hand. The parameters deduced from the genetic analysis, and their evolution over time, allowed to represent the current polymorphism and its evolution for an anonymous neutral gene with no mutation. For all analyses, the PEDIG software ([1], http://www-sgqa. jouy.inra.fr/diffusions/htm) was used.

3.1. Demographic analysis

Demographic parameters were computed taking into account "useful" off-spring only, *i.e.* offspring kept for breeding. Generation lengths were computed in the four pathways (sire-sire, sire-dam, dam-sire and dam-dam) as the average age of parents at the birth of their offspring. In order to asses their evolution over time, these parameters were computed for two cohorts: useful offspring born from 1996 to 2000, *i.e.* the youngest animals in the file, and those born from 1985 to 1989. The respective contributions of the flocks to the reference female population *via* the paternal side was analysed by simple counting: the contribution of a given flock was the number of female offspring having its sire born in this flock. The flock origins of rams progeny tested for AI were analysed in the Berrichon du Cher, Blanc du Massif Central and Limousin only: the other three breeds were excluded here, due to no (Roussin de La Hague, Solognot) or very little (Charollais) use of AI. Due to the small number of rams progeny tested each year (see Tab. I), the number of birth years considered for this analysis was larger for the rams than for the ewes, including all rams born from 1990 to 2000.

3.2. Pedigree completeness level

For the whole file, the proportion of animals with both parents known was computed by simple counting. For any ewe from the reference population, the equivalent complete generations traced (*EqG*) was computed as the sum over all known ancestors of the terms ($1/2^n$, where n is the ancestor's generation number (parent $= 1$, grand-parent $= 2$, etc.) [10]. The pedigree completeness level of the female reference population was given as the mean of *EqG* over all ewes belonging to this group.

3.3. Probabilities of gene origin

When tracing pedigrees from the female reference population, ancestors with no known parent were considered as non-inbred and non-related founder animals. The expected genetic contribution of each founder (i) was computed as the probability (p_i) for a gene taken at random within the reference population to come from founder i [2]. The effective number of founders (f_e) is defined as the reciprocal of the probability that two genes drawn at random in the reference population come from the same founder; it was computed as:

$$f_e = 1 \Big/ \sum_i p_i^2.$$

For a given total number of founders, the more balanced their expected genetic contributions, the higher the effective number of founders.

The major ancestors (founders or not) were detected using the method proposed by Boichard *et al.* [2]. The expected marginal contribution (q_j) of each major ancestor (j) was computed as its expected genetic contribution independent of the contributions of the other ancestors (see [2] for details). The effective number of ancestors (f_a) was computed in a similar way to the effective number of founders:

$$f_a = 1/\sum_j q_j^2.$$

By nature, the effective number of ancestors (f_a) is lower than the effective number of founders (f_e), and the difference between these effective numbers is due to bottlenecks between the animals analysed (the reference population) and their founders [2].

3.4. Inbreeding and relationship

Computing coefficients of inbreeding and relationship is much more sensitive to the pedigree completeness level than computing effective numbers of founders or ancestors [2]. For this reason, and due to a too large number of unknown sires (see next), the Blanc du Massif Central was excluded from these analyses. For the other five breeds, individual coefficients of inbreeding were computed, using the method by Van Raden [25]. The evolution of the average coefficient of inbreeding of females per birth year was observed from 1970 to 2000 and the annual increase of inbreeding was estimated by linear regression over time. Finally, the average coefficient of relationship between the animals bred in 2000 was computed. This group of animals was chosen here, because the average relationship between males and females bred provides a prediction of future average inbreeding.

4. RESULTS

4.1. Demographic parameters

Table II shows generation lengths between the animals born from 1996 to 2000 and their parents. For a given breed, the parent-offspring generation lengths were generally larger for the male offspring than for the female offspring. The only exceptions were in the Charollais and Solognot, where sire-sire and sire-dam generation lengths were equal. These two breeds showed the smallest average generation lengths, mainly due to particularly short sire-offspring generation lengths. In the other breeds, the average generation length was 5 to 11 months longer. The comparison of these results with the ones for animals born from 1985 to 1989 showed no change in the average generation length in the four breeds under selection, Berrichon du Cher, Blanc du Massif

Table II. Average generation lengths (*L*, in years) between useful offspring born from 1996 to 2000 and their parents.

Breed (see Tab. I)		BCH	BMC	CHA	LIM	RLH	SOL
Male offspring	Total No. useful offspring	81	351	665	107	49	21
	L sires-sires	4.9	4.3	2.9	3.8	4.1	2.7
	L dams-sires	4.1	4.7	4.1	4.7	4.4	4.3
Female offspring	Total No. useful offspring	848	6581	3448	2405	266	103
	L sires-dams	3.7	3.7	2.8	3.3	3.1	2.8
	L dams-dams	3.8	4.5	3.8	4.4	4.0	3.9
Average generation length over the four pathways		4.1	4.3	3.4	4.1	3.9	3.4

Central, Charollais and Limousin. In contrast, the average generation length increased by 6 months in the Roussin de La Hague and decreased by 5 months in the Solognot breed.

The distribution of the ewes by flock of origin of their sire is given in Figure 1. The least balanced distribution was seen in the two breeds with the largest numbers of flocks, Charollais and Blanc du Massif Central. For these two breeds, the sires of 80% of the ewes were provided by 25% of the flocks only, whereas in the four other breeds, for the same proportion of ewes 30 to 45% of the flocks provided sires. In fact, when the total number of flocks was large, it was possible for some flocks to contribute little or not at all to the sire population. In contrast, when this total number was small, all the flocks were found to provide sires, as it was the case for the Solognot breed, which clearly showed the most balanced contributions of flocks to paternal origins.

Table III gives some parameters characterising the selection process for AI rams. During the period considered, the global proportion of rams selected for AI over all progeny tested rams was 35, 24 and 38% in the Berrichon du Cher, Blanc du Massif Central and Limousin, respectively. For the flocks of origin of the rams, the Blanc du Massif Central and Limousin showed similar pictures: many different flocks gave birth to at least one progeny tested ram and no flock contributed more than 10% of the rams progeny tested or selected for AI. In the Berrichon du Cher, on the contrary, less than 20 different flocks contributed to the progeny tested or selected rams, and their contributions were much more unbalanced, mainly due to the very large contribution of a single flock.

4.2. Pedigree completeness level

Table IV shows the values for two indicators of the pedigree completeness level: the proportion of animals from the whole file with both parents known and equivalent complete generations traced (*EqG*) from the female
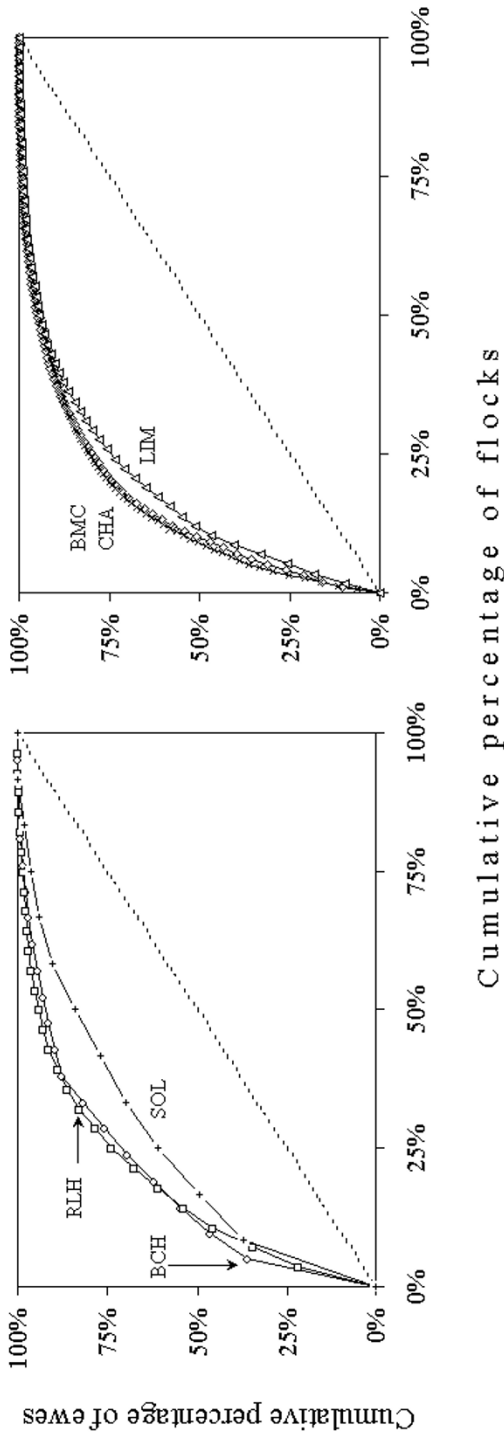
Figure 1. Cumulated percentage of ewes born from 1996 to 2000 with both parents known *versus* cumulated percentage of flocks where their sire comes from. Flocks are ranked by a decreasing contribution to sires. For the breed abbreviations, see Table I. Left: breeds with a small number of flocks, *i.e.* BCH (21 flocks), RLH (28 flocks) and SOL (12 flocks). Right: breeds with a large number of flocks, *i.e.* BMC (99 flocks), CHA (155 flocks), LIM (58 flocks). Curves for BMC and CHA overlap. The dotted thin line represents the strict equilibrium.

Table III. Contributions of flocks to the rams born from 1990 to 2000 and progeny tested or selected for AI.

Kind of rams	Rams progeny tested			Rams selected for AI		
Breed (see Tab. I)	BCH	BMC	LIM	BCH	BMC	LIM
Total No. rams	134	310	141	51	73	50
Total No. birth flocks	18	68	36	12	29	23
% of rams born in the flock contributing the most	35.1%	9.4%	7.8%	43.1%	6.8%	10.0%
No flocks contributing the most for a cumulated contribution of 50% of rams	3	10	9	2	10	7

reference population. These results are consistent, and three groups of breeds may be distinguished. First, the Berrichon du Cher and Charollais showed a good depth of pedigree, resulting from the historical wide use of AI (Berrichon du Cher) or an old tradition of genealogical recording (Charollais). The second group includes the Limousin and the two breeds under conservation, Roussin de La Hague and Solognot, with a lower proportion of animals having both parents known and an *EqG* lower by 2 to 2.6 generations in comparison with the first group. The reasons for this situation are different from one breed to the other: a lack of paternity control in some flocks (Limousin), late organisation and recognition of the breed (Roussin de La Hague) or the recent entrance of new breeders with no genealogical data into the performance recording system (Solognot). Finally, there is little knowledge of pedigree in the Blanc du Massif Central, due to the large number of flocks with no or little paternity control. All these considerations should be kept in mind when looking at the results of the genetic analysis.

4.3. Probabilities of gene origin

The results derived from probabilities of gene origin, in reference to the founder animals or to the major ancestors (founders or not), are given in Table IV. The total numbers of founders were not strictly related to the total size of the populations analysed (see Tab. I). In particular, the larger total number of founders in the Blanc du Massif Central seems to originate more from the low pedigree completeness level in this breed than from its total size. The effective number of founders (f_e) depends on both the total number of founders and the disequilibrium between their expected contributions to the gene pool. These expected contributions were found to be the most unbalanced in the Berrichon du Cher and next in the Limousin (results not shown). Compared to the Roussin de La Hague breed, the effective number of founders in Solognot

Table IV. Results of pedigree analyses. (A) Pedigree completeness level, for the whole file or for the reference population (ewes born from 1996 to 2000 and with both parents known). (B) Probabilities of gene origin for the reference population. N_{50} = number of ancestors contributing the most for a cumulated expected contribution of 50% of the genes; C_{max} = expected contribution of the ancestor contributing the most. (C) Average coefficient of relationship between reproducing animals bred in 2000.

Breed (see Tab. I)			BCH	BMC	CHA	LIM	RLH	SOL
Pedigree completeness level	Whole file	% of animals with both parents known	73%	25%	79%	58%	63%	64%
	Reference population	Maximum No. of generations traced	20	15	22	21	12	13
		No. of equivalent generations traced	6.7	2.3	6.7	4.7	4.2	4.1
Criteria derived from probabilities of gene origin		Total No. of founders	1549	15 030	3321	5524	440	442
		Effective No. of founders (f_e)	85	291	233	185	52	123
		Effective No. of ancestors (f_a)	35	144	112	69	40	49
		N_{50}	14	91	49	32	14	21
		C_{max}	10.1%	4.1%	3.8%	5.8%	6.6%	8.1%
Average coefficient of relationship		males × males	3.5	–	1.3	2.4	3.4	2.4
		females × females	2.7	–	1.0	1.6	2.2	1.8
		males × females	3.1	–	1.1	2.0	2.5	1.8

was higher by $+137\%$, whereas these two breeds had almost the same total number of founders. The two breeds with the highest values of f_e were the Blanc du Massif Central, partly due to short distances between the reference female population and the founders not allowing too much disequilibrium, and the Charollais, due to a balanced expected contribution of the founders.

The largest disequilibrium between the expected marginal contributions of the ancestors was found in the Berrichon du Cher and Limousin. In the Berrichon du Cher, a single ram was found to explain 10% of the gene pool and the value of f_a was very low. Due to a larger number of ancestors, the value of f_a in the Limousin was twice that of the Berrichon du Cher. In the Blanc du Massif Central and Charollais, no ancestor was found to have an expected contribution higher than 4% and the effective number of ancestors was rather high. In the Solognot, the low value of f_a was mainly due to the impact of a single ram, widely used within the largest flock during the 1990's. This ram was found to be the ancestor with the highest expected marginal contribution to the gene pool. The expected marginal contributions of the other ancestors were much more balanced and both the effective number of ancestors and the number of ancestors for a cumulated contribution of 50% remained higher than in the Roussin de La Hague. In this latter breed, the small difference between f_e and f_a was partly due to the fact that several major ancestors, including those that contributed the most, were also founders. The late beginning of the animal recording programme in this breed can explain that.

4.4. Inbreeding and relationship

As explained in Section 3.3, the Blanc du Massif Central was excluded from inbreeding and relationship analyses, due to a too low pedigree completeness level (see Tab. IV). Figure 2 shows the evolution of the average coefficient of inbreeding of ewes according to their birth year. Null or low values observed from 1970 to 1980 were mainly due to the lack of pedigree knowledge. Since the 1980's, the evolution has been more regular in the selected breeds than in the two breeds under conservation, because of the larger number of animals on which the average values were computed. Moreover, in the Solognot during the middle 1990's, the recording of new animals with no genealogical data led to an important decrease in the mean of the computed coefficients of inbreeding. For all these reasons, the annual rate of inbreeding was computed starting from 1980 for all breeds, and ending in 1994 for the Solognot and in 2000 for other breeds (Fig. 2). The Berrichon du Cher and Roussin de La Hague showed the largest increase in inbreeding. This increase was moderate in both the Charollais and Limousin. The Solognot showed an intermediate situation. Taking into account the generation lengths of the breeds, these annual rates of inbreeding roughly correspond to realised effective population sizes ranging between 120 (Berrichon du Cher) and 360 (Limousin).
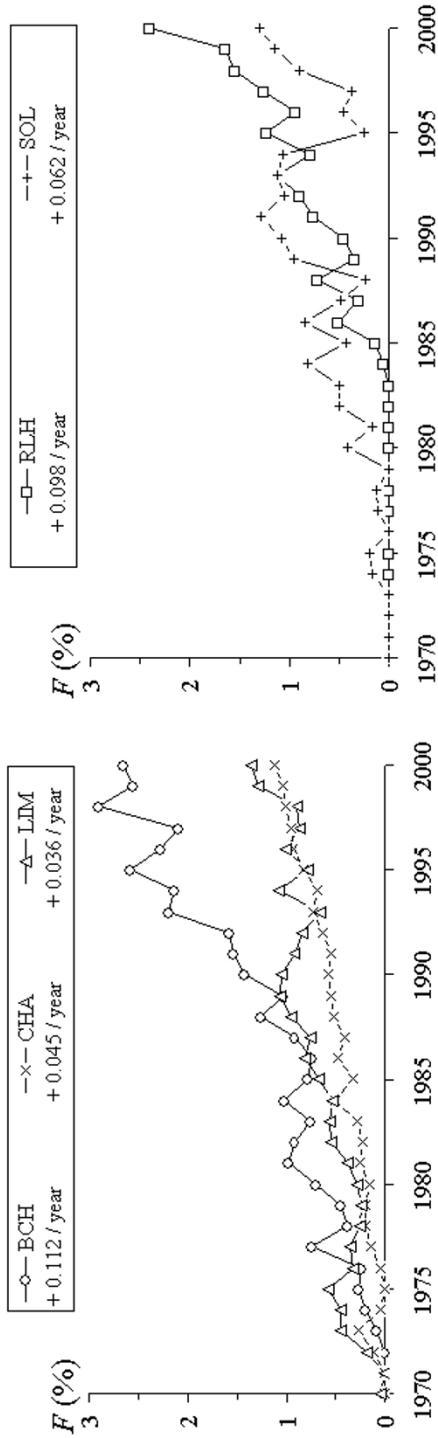
Figure 2. Evolution of the average coefficient of inbreeding (F, in %) of ewes per birth year from 1970 to 2000. Left: breeds under selection. Right: breeds under conservation. For the breed abbreviations, see Table I. In the legend, the number under the abbreviation and symbol for each breed represents the annual increase (in percentage points of percentage per year) of the average coefficient of inbreeding in females born during the period 1980–2000 (1980–1994 in SOL).

Table IV shows the average coefficients of relationship between males, between females and between males and females used as parents in 2000. For a given breed, the highest value was between males and the lowest between females. For a given category, the relationship was the highest in the Berrichon du Cher and Roussin de La Hague and it was the lowest in the Charollais. In selected breeds, the relationship between both rams and ewes qualified to be parents of new rams was found to be higher than for the whole group of male and female parents (results not shown), except in the Charollais where no difference was found.

5. DISCUSSION AND CONCLUSIONS

5.1. Comparison with other studies

The populations considered in this study were chosen due to their *a priori* differences in some characteristics: total size (from very large to endangered breeds), collective organisation for selection or conservation, development of AI, paternity control, etc. When looking at other studies, these differences should be taken into account, especially when considering other species for which both biology and technical possibilities for artificial reproduction are very different. A few studies focusing on sheep breeding can be compared to this study. Palhière *et al.* [15] studied the main French dairy sheep breeds, Lacaune and three breeds from the Pyrenees mountains. These populations were generally larger (from 18 000 to 166 000 recorded ewes), AI was widely used (from 50 to 80% of the recorded ewes), and the number of progeny tested rams per year was much larger (from 30 to 130 in breeds from the Pyrenees, up to 470 in the Lacaune). With pedigree completeness levels in the same range as in the present study, these authors found similar or smaller values for the realised effective size (from 110 to 220) and smaller values of the effective number of ancestors computed for the AI rams only (from 14 to 54). Hagger [6] studied two Swiss meat breeds: the White Alpine Sheep (WAS), which is widely used and was partly crossed with the Ile-de-France breed, and the Black-Brown Mountain Sheep (BBM), which is a smaller and closed population. These breeds share some peculiarities: better and deeper pedigree knowledge than in the present study, no use of AI and a weak selection pressure. Under such conditions, this author found values of effective numbers of founders or of ancestors similar to the highest values in the present study, and values of the realised effective size similar to the lowest value in the present study (111 in BBM) or much higher (900 in WAS, partly due to crossing).

5.2. Cases of breeds under selection

In this study, within the group of breeds that have a selection programme, the Berrichon du Cher and Charollais breeds were found to have a similar and

good pedigree knowledge, which makes the comparison of their values for criteria based on genealogical analysis easy. These two breeds showed marked and interesting differences. In the Berrichon du Cher, the different steps of the selection programme are well coordinated. Especially, the majority of the young rams to be performance- and progeny-tested are sons of previously tested AI rams, and AI rams are widely used in the flocks. However, the total number of Berrichon du Cher recorded ewes was around 3100 only, and a single flock was found to contribute to more than 35% of the ewes' sires (see Fig. 1) and to more than 40% of the AI rams (see Tab. III). On the contrary, in the Charollais breed, AI rams are not so widely used after having been progeny tested. The sire-son generation length was found to be shorter than what it should be after progeny testing, indicating that the ram selection process is not as efficient as it could be. When looking at the results of the pedigree analysis, the effective numbers of founders or of ancestors in the Berrichon du Cher were found to be around 3 times lower than in the Charollais, and the rate of inbreeding and the average coefficients of relationship were found to be around 2.7 times higher. These large differences in the variability of gene origins and in the increase of homozygosity are mainly due to an intense selection on a small nucleus of animals in the Berrichon du Cher breed, on the one hand, and to a low selection pressure in the Charollais breed, on the other hand.

The Limousin breed showed an intermediate situation between the latter two breeds. Demographic parameters indicate that the selection and the use of rams are almost as efficient as in the Berrichon du Cher breed, but with much more balanced contributions of the different flocks, leading to less concentrated gene origins. The value of the rate of inbreeding for the Limousin, which was found to be the lowest in this study, should be interpreted as the consequence of both a good genetic management and a lower pedigree completeness level. Finally, the values of the different criteria observed in the Blanc du Massif Central have to be considered, taking into account the very low pedigree knowledge. The main result provided by the study of this breed is probably the fact that, despite the lack of paternity control, a collective programme can be organised. This involves performance-testing many young rams to become sires of the next generation and also to manage gene diffusion in the population.

5.3. Cases of breeds under conservation

The other two breeds in this study are under conservation. As the amount of pedigree information available is the same, the results can be compared in the context of different management rules. For a long time, the Solognot was managed with a well-defined goal, with demographic and genetic rules and using a collective rearing station. Such a strategy does not exist for the Roussin de La Hague breed, since management decisions are made by each individual flock. The present study is more comprehensive for the Solognot

than an earlier study focusing mainly on the male population [3]. It confirms that the breeders apply the rules of the conservation programme, despite the practical and financial consequences of the exchanges between flocks of a large number of rams. The balanced contributions of the flocks to the ram population is due to both the rotational mating scheme and the use of a rearing station which facilitates the provision of rams from different flocks. Moreover, the homogeneous environmental conditions provided to all young growing rams leads to a reduction in the performance differences due to their flock of origin. The low value of the sire-son generation interval indicates that the replacement of rams is fast enough to avoid a too large family size for a given ram (although some exceptions were found). The Roussin de La Hague has an actual population size 8.8 times larger than the Solognot, and the number of ewes have been tripled in the last 15 years. Despite this, all the results obtained from the pedigree analyses were much more favourable for the Solognot breed. The Solognot was found to have an effective number of founders more than twice that of the Roussin de La Hague. The annual rate of inbreeding was higher in the Roussin de La Hague than in the Solognot (+58%), despite a longer average generation length (+13%). The average coefficients of relationship between animals bred in 2000 were higher in the Roussin de La Hague (+22 to +42%, according to the group of animals considered). These differences may be largely explained by both more unbalanced contributions of flocks to the ram population and fewer exchanges between flocks in the Roussin de La Hague breed. Such a comparison confirms the value of the genetic rules applied to manage the Solognot breed.

5.4. Practical implications

The results obtained in this study highlight the importance of the collective organisation of breeders for the management of a breed, both under selection or conservation programme. Under selection, collective organisation is a key-point to creating and spreading genetic gain. However, a too intense selection will reduce the within-population genetic variability, as shown by the Berrichon du Cher. The selection programme for this breed should take the management of the genetic variability into account, by enlarging the selection basis and purchasing rams with more diversified origins. Due to the high level of organisation of this breed, some rules could also be implemented, such as managing rams into different reproduction groups and applying a within-group selection of rams. Such rules were found to be efficient for preserving the variability and avoiding a too high rate of inbreeding in the case of the intensively selected Lacaune dairy sheep breed [15]. These rules, however, should be adapted to the small number of Berrichon du Cher rams that are progeny tested each year. On the contrary, a more rigourous selection and a wider use of AI in the Charollais breed could be undertaken. With the large

genetic basis of this breed and by applying some simple rules, as in the Lacaune breed (see above), the selection process could become more efficient with little reduction in genetic variance. The situation of the Roussin de La Hague breed gives cause for concern. Effective decisions should be quickly taken for a more collective organisation of this breed, putting much emphasis on both more diversified origins of rams and more rational exchanges of rams between flocks.

All these considerations about genetic variability are of particular importance in the current context of the national programme for improving the genetic resistance of sheep to scrapie, which involves (i) the elimination of the VRQ allele at the PrP locus and (ii) selection for the ARR allele at this locus and the promotion of ARR/ARR rams [16]. It is well known that the selection on a single gene could lead to bottlenecks in a population, as illustrated by the case of the eradication of the allele for halothane susceptibility in the Landrace Français pig breed during the 1980's [9]. From a national survey, the four selected breeds studied here were found to have different allele frequencies at the PrP locus [16, 17]: the frequencies of the ARR allele were estimated to 0.81, 0.41, 0.40 and 0.25 in the Berrichon du Cher, Limousin, Charollais and Blanc du Massif Central, respectively. Therefore, the selection on the PrP locus should have no or little undesired effect on the genetic variability in the Berrichon du Cher, whereas the selection schemes of the other breeds should be adapted [17], especially for the Charollais. The first (and unpublished) results about allelic frequencies at the PrP locus within breeds under conservation indicate that the situation seems to be favourable in the Solognot and unfavourable in the Roussin de La Hague (Palhière and Orlianges, personal communication). These results have to be confirmed on large samples but already strengthen the urgent need for Roussin de La Hague breeders to move towards the collective management of their breed.

ACKNOWLEDGEMENTS

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