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High prolificacy in Belle-Ile sheep (Brittany, France): major effects of a putative single gene and the A^{wh} colour gene on ovulation rate and litter size

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Abstract – Ovulation rate (OR) and litter size (LS) were recorded in 72 ewes from a traditional sheep population native to Belle-Ile en Mer, France (BI) from 1986 to 1996. Mean, range and repeatability of OR were: 2.54 ± 1.1 ($n = 494$), 1–8 and 0.8, respectively, whereas, for LS, they were: 2.23 ± 1.0 ($n = 146$), 1–7 and 0.2, respectively. OR is significantly influenced by age, number of OR, maximum OR in the dam (≤ 3 versus > 3), sire and colour of the fleece (white versus black pattern). OR was also recorded in Charmoise ewes (CH), their F1 progenies with four BI rams and BI ram × F1 backcross ewes (BC). OR range and OR mean in CH ewes, four F1 progenies and BC ewes were: 1–2 and 1.2, 1–2 and 1.2, 1–2 and 1.3, 1–3 and 1.9, 1–4 and 2.3, 1–6 and 2.8, respectively. OR repeatability in CH, F1 and BC were 0.16, 0.45 and 0.71, respectively. The large variation in ovulation rate and litter size combined with high repeatabilities, the familial transmission of a high ovulation rate and the observations in F1 and BC support the hypothesis of a single gene with a large mean effect on ovulation rate and litter size segregating in the population. © Inra/Elsevier, Paris

sheep / ovulation rate / litter size / major gene / colour gene

Résumé – Prolificité élevée en mouton de Belle-Île-en-Mer (Morbihan) : effets majeurs d'un possible gène de prolificité et du gène de couleur A^{wh} sur le taux d'ovulation et la taille de portée. Le taux d'ovulation (TO) et la taille de portée (TP) ont été mesurées chez 72 brebis issues d'une population ovine traditionelle de Belle-Ile en Mer (BI) entre 1986 et 1996. La moyenne, la gamme et la répétabilité de TO ont été respectivement de : 2,54 ± 1,1 ($n = 494$), 1–8 et 0,8 alors que pour TP, elles ont été respectivement de : 2,23 ± 1,0 ($n = 146$), 1–7 et 0,2 respectivement. TO est significativement influencé par l'âge, le rang d'ovulation, le TO maximal de la mère (≤ 3 vs > 3), le père et la couleur de la toison (patron blanc vs noir). Le TO a aussi été enregistré chez des brebis de race Charmoise (CH), leurs descendances F1 issues de quatre béliers BI, ainsi que des brebis (BC) issues de croi-

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sement en retour entre brebis F1 et un bélier BI. La gamme de TO et le TO moyen chez les brebis CH ont été respectivement : 1–2 et 1,2 ; successivement pour chacune des quatre descendances F1 respectivement :1–2 et 1,2 ; 1–2 et 1,3 ; 1–3 et 1,9 ; 1–4 et 2,3 et pour les brebis BC respectivement : 1–6 et 2,8. La répétabilité du TO était de 0,16 chez les brebis CH, 0,45 chez les brebis F1 et 0,71 chez les brebis BC. L'étendue des gammes de variations de TO et de TP combinée à leur forte répétabilité, le caractère familial de la transmission d'un TO élevé et les observations dans les croisements F1 et BC militent en faveur de l'hypothèse d'un gène majeur ségrégeant dans cette population et ayant un effet important sur la taille de portée et le taux d'ovulation. ©Inra/Elsevier, Paris

ovin / taille de portée / taux d'ovulation / gène de coloration / gène majeur

1. INTRODUCTION

Natural high ovulation rate and litter size in sheep are commonly related to two genetic determinants.

On the one hand, in Booroola sheep, Piper and Bindon [30] reported that a single gene had a large effect on prolificacy. Since then, several other breeds have been reported to present similar major genes: Icelandic sheep [18], Cambridge sheep [16], Javanese sheep [5], Creole sheep [23], Oluska sheep [27], Romney sheep [6], Cambridge and Beclare breeds [15]. Their effects have generally been considered as additive, except for Romney sheep where Davis et al. [7, 8] have reported that the Inverdale prolificacy gene is located on the X chromosome and is associated with infertility in homozygous carrier ewes.

On the other hand, the high prolificacy exhibited by some other breeds, such as Romanov [9], Finnish [24] or D'Man [20] breeds, is the result of a long-term selection with gradual accumulation of favourable genes with small effects.

A traditional sheep population reared in small family flocks was described on the island of Belle-Ile en Mer (Morbihan district, Brittany, France) [25]. Morphological and reproductive traits, i.e. poor conformation, coarse black or white fleece, frequent triplets and quadruplets in some ewes distinguished these sheep from the others on the island.

These sheep are probably the surviving descendants of a population called 'Race de Deux', i.e. 'Twin Breed', located in the continental part of the Morbihan district [10]. Unlike the surrounding sheep populations of Brittany at the end of the 19th century, ewes of this population frequently lambed twins (as the name implies), and sometimes triplets. They were reared in small flocks of three or four ewes because of local regulations [19]. This small-flock sheep farming tradition could have promoted (and preserved) a higher prolificacy through both previously described genetic mechanisms, arguing therefore for further research.

Heuzé [17] reported a specific origin to that population, i.e. the importation of prolific 'Flandrine' ewes (Dutch origin) to Morbihan in 1760. Thomas Corneille (cited by Magne [22]) reported the ability of Flandrine ewes to have usually three lambs and sometimes four, five, six or occasionally seven lambs per litter.

In 1985, interviews of 16 owners were conducted about the careers of their ewes. According to their declarations, the mean litter size was estimated to be 2.16 ($n = 226$); 32 % of the litters were triplets or higher. In a longitudinal survey conducted for three successive lambing periods (1986–1988), mean litter size was 2.0 in 170 litters (26 litters from ewe lambs), with 20 % of litters being triplets or higher.

The transmission of a higher prolificacy was noted to affect more specifically some families where high litter size was repetitive in affected ewes. Looking for possible environmental or chemical enhancing factors of litter size, it was observed that the feeding conditions were poor, specially without any flushing diet, and that no artificial treatments (like intra-vaginal progestagen pessaries, combined with PMSG at pessary removal) were used. Moreover, the ewes were bred in small units, therefore promoting inbreeding, which is supposed to depress fecundity.

Together with previously described historical observations, these characteristics argue for further investigation into the presence of a putative gene influencing ovulation rate in this population of sheep. Therefore the objective of this study is to describe the prolificacy of this traditional population and investigate the possibility of a major gene influencing ovulation rate.

2. MATERIALS AND METHOD

An experimental flock consisting of three ewes (C, F and G), three ewe lambs (D, E and H) and two rams (R1 and R2) has been established since 1986 at the Veterinary School of Nantes to assess the reproductive traits in this population of sheep. In 1988, three more ewes (A, B and I) and one ram (R4) were added to the flock. All the foundation animals came from the same flock and are therefore supposed to be related, except two ewes (Dam A and F) from a different origin. The ewes B, C and I were 3–4 years old and A, F and G were more than 6 years old when entering the flock.

The number of ewe lambs (with at least one coelioscopy) born in 1987, 88, 89, 90, 91 and 92 were 3, 11, 6, 10, 11 and 24, respectively. Ewe lambs were first mated in their second breeding season, at the age of 18–20 months. All female progeny were kept, resulting in 92 registered females in autumn 1993. Sixty ewes had at least one lambing at the Veterinary School. Four additional rams originating from the ewes exhibiting the highest ovulation rate were kept for reproduction. Ovulation rate (OR) was assessed by coelioscopy [28] 4–7 days after ovulation.

To obtain a sufficient number of ewe lambs from each ram, a different ram was used each year: R1 in 1986, R2 in 1987, R4 in 1988. However, R5 was used in 1989, 1990 and 1991. A varying number of coelioscopies were carried out until 1989, depending on the onset of the breeding season. From October 1989, ewe lambs born in the spring of the previous year (aged 18–20 months) had three coelioscopies (two before mating and one afterwards), whereas adults had two (one before mating and one afterwards). Ewe lambs born in the spring were assessed as to whether puberty onset occurred during the observation period of the other females.

Belle-Ile (BI) rams were also used in crossing with Charmoise (Ch) ewes. Prolificacy of the Charmoise breed is low, averaging about 122 % in adult ewes (UPRA Charmoise, cited by Perret [29]).

Statistical analysis were performed using Statview 4.0 software (Abacus Concept [1]) and SAS 6.11 [32]. Repeatability estimates (and their standard deviations) were obtained for ovulation rate and litter size by inter-class and intra-class correlations according to the methods described by Turner and Young [33] using mixed models to obtain between and within ewe components of variance. The data set used for the calculation was limited to OR from ewes of ≤ 5 years of age and at least two records and a maximum of three records per year, resulting in 415 records from 64 ewes.

A general linear model was performed to estimate the effect of different factors on ovulation rate and litter size. Because of the small number of offspring per dam, the genetic effect of the dam was indirectly accounted through a classification in two classes, based on its maximum ovulation rate record: three or less than three for the first class and four or more for the second. For this classification, at least five records were available for each ewe (except for ewes A and I on which only two ovulation and one litter size records were available). As two colour patterns (black and white) existed in the flock and because the white fleece dominant colour gene is known to depress fecundity [18], colour was considered in the model although it was not recorded on every ewe.

Finally, the model for ovulation rate was tested for fixed effects of age, coelioscopy number, year, sire, maximum OR in the dam, colour pattern and interactions of colour × maximum OR in the dam and colour × sire interaction. The general linear model for litter size used the same variables, except the coelioscopy number variable. The number of records used in the analysis were 362 for ovulation rate (from 54 ewes) and 90 for litter size (from 49 ewes).

Considering the possibility of a major gene influencing the ovulation rate in this population, a segregation criterion was being looked for. In the absence of any standard population, an analysis of the pedigrees and observations of purebred and crossbred progeny performances was implemented in order to propose a typing of the rams (carrier/non-carrier).

3. RESULTS

3.1. Ovulation rate

Mean ovulation rate in 494 records (72 ewes, 2 to 17 records each) was 2.54 ± 1.1 (ranged from 1 to 8). The percentage of ovulation rate of one, two, three, four, five and six or more was 12.7, 43.5, 33.4, 7.2, 4.4 and 2.8, respectively. At the individual level, the mean ovulation rate averaged 2.60 ± 1.0 in ewes with at least three records and aged ≥ 18 months ($n = 69$). Its frequency distribution is given in *figure 1*.

Mean ovulation rates are given in *table I*. Ovulation rate at first parity (2.2) was lower than at later parities (2.5) (ANOVA, $P < 0.05$). Ovulation rate increased significantly with time of season during the second breeding season (paired comparison, $P < 0.02$). Estimated intra-year and between-year repeatabilities of ovulation rate were, respectively, 0.79 ± 0.04 and 0.70 ± 0.05 in 64 ewes ($n = 415$).

In the model (*table II*, $R^2 = 0.31$), significant effects were found for age, coelioscopy number, sire, maximum OR in the dam, colour pattern and interaction of colour × maximum OR in the dam, whereas year effect and colour × sire interaction were found to be non-significant. Colour × sire interaction was deleted from the model, but not year effect.

Considering genetic factors, the effects of sire and maximum OR in the dam were significant and large as estimated by the model: the difference in LS means was up to 1.2 between progenies of R4 and R1 and almost 0.5 between ewes from the two different classes of maximum ovulation rate in the dam. White colour gene appeared to depress ovulation rate (–0.45) in white compared to black ewes. Dam effect and colour effect showed an interaction: the upper class of dam ovulation rate had a strong effect on ovulation rate in black ewes (+ 0.9 compared to lower class), but had no effect in white ewes.

Because of long careers, some ewes contributed for a quite larger number of ovulation rates compared with others in the data set. To reduce their weight, the model was calculated on a subdataset ($n = 306$ versus

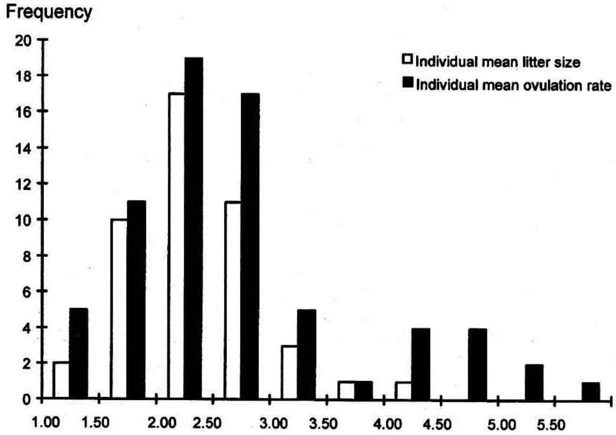

Figure 1. Distribution of individual mean ovulation rate ($n = 69$ ewes, at least three records per ewe) and individual mean litter size in Belle-Ile ewes ($n = 45$, at least two records per ewe).

Table I. Mean ovulation rate, mean litter size in Belle-Ile ewes.

Coelioscopy	Ovulation rate									Litter size		
	Age et coelioscopy in months									Age at lambing, y		
	7		20			32		44		2	3	4
number	1st	2nd	1st	2nd	3rd	1st	2nd	1st	2nd			
Mean	2.1	2.0	2.1	2.5	2.7	2.6	2.7	2.9	2.8	1.9	2.5	2.6
s.d.	0.9	0.9	0.9	1.1	1.4	1.2	1.0	0.8	0.8	0.8	0.8	0.8
n	75	39	77	65	61	51	43	48	35	48	35	22
Mean diff.	–		0.34	0.23		–		–		0.40	0.17	
P value	–		< 0.001	0.015		–		–		0.07	0.18	

n = 362) limited to a maximum of three records per ewe and per year until the maximum age of three. The model gave the same pattern as that of the original data set.

A model built on a larger data set (n = 427) but not including a colour parameter, presented a very similar pattern for the respective effects of age, coelioscopy number, year, sire and maximum ovulation rate in the dam.

3.2. Ovulation rate of Belle-Ile first and back crosses

The number of coelioscopies and the age of ewes in which they were performed, for 19 Ch, 31 F1 and 14 back-cross (F1 × BI) ewes, are presented in *table III*, as well as the sire identity and the mean and range of ovulation rate. Only F1 ewes sired by R3 and R5 were back-crossed with ram R5.

Estimations of ovulation rate repeatability were 0.16 ± 0.12 in 18 Charmoise ewes (n = 74), 0.45 ± 0.10 in 31 F1 ewes (n = 153) and 0.71 ± 0.11 in 14 F2 ewes (n = 73). Due to unbalanced F1 ewe records in the different progenies with respect to age (*table III*), an estimation of repeatability was also calculated only with the records of their second breeding period and was found to be 0.58 ± 0.10 (n = 89).

In Charmoise ewes and in R1 and R2 F1 progenies, the ovulation rate was similar in range (OR = 1 or 2) and mean (1.2). Within the progeny of R3, an ovulation rate of 3 was recorded in two out of five F1 ewes. Within the progeny of R5, an ovulation rate of 4 was recorded in two out of five F1 ewes at the age of 7 months, whereas a maximum ovulation rate of 3 was only recorded in the following breeding periods. Mean ovulation rate in R3 and R5 F1 progenies was 0.9 points higher than in Charmoise dams.

In 14 back-cross ewes, seven gave an ovulation rate of 4 or more, whatever the ovulation rate of their dam. Distribution of ovulation rate in 14 backcross ewes (n = 73)

Table II. Effects of age, coelioscopy number, year, sire, maximum ovulation rate in the dam, colour of the fleece, interaction colour × maximum ovulation rate in the dam on ovulation rate ($n = 362$) and litter size ($n = 90$) estimated by means and least square means using general linear models procedure.

		Ovulation rate				Litter size			
Factor	Class definition	No. of records (ewes)	Means (s.d.)	L. S. means	*P* value	No. of records (ewes)	Mean (s.d.)	L. S. means	*P* value
Age (years)					0.0003				0.1
	1	84 (46)	2.26 (0.90)	1.99					
	2	155 (53)	2.65 (1.07)	2.46		42 (42)	2.0 (0.9)	1.9	
	3	70 (30)	2.83 (1.17)	2.88		27 (27)	2.6 (0.9)	2.4	
	>3	53 (16)	3.00 (1.32)	3.20					
	4					13 (13)	2.6 (0.9)	2.6	
	>4					8 (6)	2.8 (1.2)	3.0	
Coelioscopy number in the breeding season					0.02				
	1st	154 (54)	2.49 (1.08)	2.43					
	2nd	137 (54)	2.75 (1.15)	2.65					
	>2nd	71 (50)	2.76 (1.10)	2.81					
Year					0.3				0.8
	1988	8 (3)	1.75 (0.46)	2.83					
	1989	29 (13)	2.00 (0.65)	2.42		4 (4)	1.8 (1.0)	2.4	
	1990	59 (19)	2.78 (0.86)	2.85		8 (8)	1.9 (0.6)	2.6	
	1991	68 (30)	2.60 (1.00)	2.61		12 (12)	2.6 (1.0)	2.9	
	1992	93 (46)	2.68 (1.15)	2.62		16 (16)	2.3 (1.0)	2.3	
	1993	105 (43)	2.81 (1.32)	2.47		23 (23)	2.4 (0.9)	2.4	
	1994					27 (27)	2.4 (1.0)	2.3	
Sire					0.0003				0.7
	R1	26 (3)	2.00 (0.69)	1.98		9 (3)	2.3 (0.9)	2.5	
	R2	45 (4)	2.42 (0.58)	2.44		19 (6)	2.2 (0.8)	2.2	
	R4	51 (6)	3.47 (1.50)	3.22		17 (6)	2.7 (1.3)	3.5	
	R5	240 (41)	2.58 (1.04)	2.89		45 (31)	2.2 (0.9)	2.8	
Maximum OR in the dam					0.0001				0.05
	3 or < 3	240 (34)	2.41 (0.72)	2.39		59 (29)	2.2 (0.8)	2.3	
	> 3	122 (20)	3.10 (1.54)	2.87		31 (17)	2.5 (1.2)	2.7	
Colour					0.001				0.2
	black	184 (30)	2.90 (1.36)	2.86		35 (21)	2.5 (1.2)	2.7	
	white	178 (24)	2.38 (0.71)	2.41		55 (25)	2.2 (0.8)	2.3	
Colour * maximum OR in the dam					0.001				0.0005
	Black * 3 or < 3	91 (14)	2.40 (0.80)	2.42		17 (11)	1.8 (0.9)	2.1	
	Black * > 3	93 (15)	3.39 (1.60)	3.30		18 (10)	3.1 (1.1)	3.2	
	White * 3 or < 3	149 (19)	2.42 (0.67)	2.37		42 (18)	2.4 (0.7)	2.5	
	White * > 3	29 (6)	2.21 (0.86)	2.44		13 (7)	1.8 (0.8)	2.2	

and their mother (seven ewes, $n = 65$) is given in *figure 2*. The range of ovulation rate (1–6) is enlarged compared to F1 range. The mean ovulation rate in R5 BC progeny was 0.7 points higher than in F1 dams.

From these results and referring to the average performance of the dams, R3 and R5 appeared to be very different from R1 and R2 for their effect on the OR of their F1 progenies and the effect of R5 on OR mean appeared to be similar, even lower, in its back-cross progeny as in its F1 progeny. These statements are integrated in the progeny analysis of rams R1, R2, R3 and R5 here below.

3.3. Litter size in Belle-Ile ewes

Average litter size in 126 records (60 ewes, 1–5 records each) was 2.23 ± 1.0 (ranged from 1 to 7). The percentage of single, twin and triplet/more litters was 24.0, 39.7 and 36.3 %, respectively. At individual level, the mean litter size averaged 2.19 ± 0.62 in ewes with at least two records ($n = 45$). Its frequency distribution is given in *figure 1*.

Mean litter size at successive lambings is given in *table I*. The estimate of repeatability was 0.22 ± 0.13 in 38 ewes ($n = 93$). Litter size of adult ewes (2.5) was 0.4 lambs/litter higher than that of 2-year-old ewes.

In the model (*table II*, $R^2 = 0.33$), only maximum OR in the dam and the interaction of colour × maximum OR in the dam had a significant effect on litter size.

3.4. Progeny analysis

Ovulation rate and litter size in the foundation ewes and their daughters are presented in *table IV*. In order to propose a typing of the rams with respect to a putative gene, classification criteria of the different genotypes were based on the following considerations: ewes A, a1, a2, B, b1 and C recorded

Table III. Number of coelioscopies and ovulation rate in Charmoise ewes and Belle-Ile crossings.

Genotype	Sire	No. of ewes	No. of coelioscopy at the age of			Total number of coelioscopy	Ovulation rate	
			7–8 months	18 months	≥ 26 months		Mean	Range
Ch	–	19	0	0	3–6	74	1.2	1–2
Ch × BI	R1	12	0	2–4	0	32	1.2	1–2
Ch × BI	R2	9	0	2–4	0	27	1.3	1–2
Ch × BI	R3	5	0–2	3	3–6	45	1.9	1–3
Ch × BI	R5	5	2–4	3	4	49	2.3	1–4
F1 × BI	R5	14	0–2	2–3	0–2	73	2.8	1–6

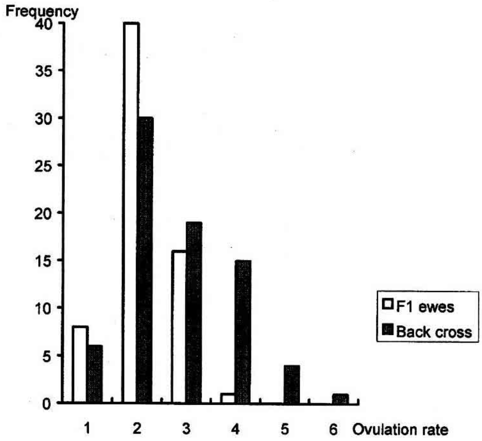

Figure 2. Distribution of ovulation rate (0–3 records per breeding season) in seven Charmoise × Belle-Ile ewes, aged 7–44 months (*n* = 65) and their 14 back-cross F1 × Belle-Ile daughters, aged 7–32 months (*n* = 70).

the highest ovulation rates (5, 6, 7 or 8) and were therefore assumed to be carrier of the putative gene. Daughters with low ovulation rates, i.e. one, two and sometimes three (e.g. b4, c1, c2 and c4) were considered as representative of non-carriers. Between these two extreme profiles, it seemed difficult to propose relevant criteria to separate heterozygous carriers from non-carriers on the one hand and heterozygous from homozygous carriers on the other.

In F1 progenies, R3 and R5 improved the OR mean and range in their progeny, whereas R1 and R2 did not. Therefore R1 and R2 were considered as non-carriers. This classification is not contradictory to their pure-bred progeny performances (*table IV*) where none of the daughters repeated the highest performance of the dam with the highest profile (C).

Ram R5 could not be a homozygous carrier since its mates, ewes B and E, gave at least one low rating daughter (b4 and e5). Considering the performances of its progeny in F1 and BC ewes, and a higher maximum OR in some pure-bred offspring compared with that of their dam (b1/B and e4+e6/E), it was therefore considered as a heterozygous carrier.

Ram R3 was the son of ewe C and ram R1 and gave only cross-bred progeny. The progeny consited of five F1 daughters exhibiting a very similar pattern to that of R5 F1 progeny with respect to OR mean and OR range. It was also designated as a heterozygote carrier.

Ram R4 gave only three pure-bred daughters with foundation ewes. As R5, ram R4 could not be considered a homozygous carrier since its mate G produced one daughter with a low ovulation rate (g1). On the other hand, as its daughters (a1 and a2) repeated the very high ovulation rate of their mother and due to its estimated effect in the model, it was also assumed to be a heterozygous carrier.

Considering R1 and R2 as non-carriers and R4 and R5 as heterozygote carriers, intra- and between-year OR repeatabilities in their progeny were estimated and found to be 0.59 ± 0.06 and 0.43 ± 0.14, respectively, in R1+R2 progeny (*n* = 110, 15 ewes) and 0.79 ± 0.04 and 0.67 ± 0.05, respectively, in R4+R5 progeny (*n* = 305, 49 ewes).

4. DISCUSSION

In the different breeds where a major gene is reported to have an effect on ovulation rate and litter size, the presence of such a gene is supported by the following

Table IV. Successive ovulation rates (ovulation rate as ewe lambs in italics) and litter size (in brackets) of the foundation ewes and their progenies according to the sire.

Sire	Dam	Ovulation rate (litter size) in the dam	Daughter	Ovulation rate (litter size) in the daughter
R1	C	4,4,5,(3),4,(4),3,(1),1,5,4,(1)	c1	2,1,2,(1),1,1,1,(1)
	F	3,3,3,(2),2,2,(2),2,(1),2,2,3,(1)	f1	1,2,(3),1,2,2,(2),2,2,2,2,(3)
			f2	2,2,2,(2),3,2,3,(3),3,3,3,3,(3),3,2,(3)
R2	C	4,4,5,(3),4,(4),3,(1),1,5,4,(1)	c2	1,2,1,(1),2,2,2,1,(2)
			c3	2,2,2,3,3,3,(3),2,4,(3),3,4,(3)
			c4	1,2,3,(2),1,2,2,2,(2)
	D	*1,1* - 1,1,2,(2),2,1,2,(2)	d1	1,1,2,(1),2,3,2,2,2,2,(2)
			d2	1,1,2,(1),2,2,3
	E	*2,1,1* - 2,2,2,(2),3,2,2,(2),3,2,3,(3)	e1	1,2,2,(2),2,2,3,3,(3),2,3,(2)3,3,3,(3),3,3,(3)
			e2	2,2,2,(1),3,2,3,(2),2,3,(1)
R4	A	5,6,(7)	a1	*3,3* - 3,4,5,(4),4,5,(2),4,5,(3),4,7,(5)
			a2	*3,3* - 5,4,5,(4),6,6,(5),6,6,(4),6,7,(5)
	G	4,2,4,(2),2,1,3,(3),3,3,2,4,(1)	g1	*1* - 2,1,2,(2),2,2,(2)
R5	B	4,4,4,5,(3),4,4,(2)	b1	*5,4* - 4,4,5,8,5,(4),4
			b2	*2,2,2* - 2,3,3,(1),3,3,(3),3
			b3	*4,4* - 3,4,5,(3)
			b4	*1,1* - 2,1,2,2
	C	4,4,5,(3),4,(4),3,(1),1,5,4,(1)	c5	*2,3,2* - 2,3,3,(3)
	E	*2,1,1* - 2,2,2,(2),3,2,2,(2),3,2,3,(3)	e3	*2,2, 2* - 3,3,3,(2),2,3,(3),2,3,(3)
			e4	*1,2* - 2,4,2,(2),3,2,(2),3
			e5	*1* - 2,2,2,(3),2
			e6	*2,3* - 3,2,2,3,3,(4),3,2

criteria: the observation of a high variation between individuals for fecundity traits within a breed, population or family; a high repeatability of the ovulation rate and litter size and Mendelian transmission of higher fecundity characteristics to the progeny.

The present study followed the observation made by Malher and Denis [25] of an unusually high prolificacy in a population of indigenous sheep in France. The present findings confirmed the high litter size and presence of a wide range of variation in litter size in this population. Ovulation rate in this population was shown to have a high mean level, a wide variation, and a high repeatability, supporting the hypothesis that a major gene with a large effect on ovulation rate exists in this population.

Ovulation rate repeatability estimates in Belle-Ile and F2 ewes were high and similar to that in Javanese (0.65–0.80, Bradford et al. [5]), Cambridge (0.72, Hanrahan [14]) or Icelandic sheep (0.64–0.77, Eypórsdóttir et al. [11]), all of which are breeds suggested to have a single gene responsible for a high fecundity. In contrast, the repeatability estimate in Charmoise ovulation rate appeared to be low, whereas that in F1 ewes appeared to be intermediate. Differences between repeatabilities in the two categories of Belle-Ile progenies (R1 + R2 versus R4 + R5) as well as between F1 and backcross ewes could be interpreted using the hypothesis that R1 and R2 were non-carriers and R3, R4 and R5 were heterozygous carriers.

The estimate of litter size repeatability (0.22) was intermediate between estimates for genotypes with a major gene: 0.35 in Javanese [5] 0.32 in Icelandic sheep [18] and for other prolific genotypes: 0.15 in DLS (Dorset * Leicester * Suffolk synthetic line) and DLS * Finnish crosses [12], 0.12 in Romanov breed [31], 0.11 in D'Man ewes [4].

In Charmoise ewes, no ovulation rate of three has ever been described. In Charmoise × Belle-Ile cross, the progeny of two rams (R3 and R5) out of four exhibited at least one ovulation of three. This result can be therefore interpreted as an effect of the putative major gene in R3 and R5 progeny. Mean ovulation rate was clearly higher in progeny of the carrier rams compared with Charmoise dam records (+ 0.9) and in the R3 BC progeny (+ 0.7) compared with the F1 dams.

The effect of the gene on the range of ovulation rate in the crossbreeds (1–6) seemed rather limited compared to that in Belle-Ile ewes (1–8). Bindon and Piper [3] indicated that the effect of a major gene possibly depends on the genetic background in which it is expressed. It should also be noted that the records ranging from 1 to 6 in the backcross ewes were only collected during the three first breeding periods, whereas longer careers were available in Belle-Ile ewes.

In Belle-Ile sheep, black is determined to be recessive to white since no white offspring was ever obtained from black parents, whereas black offspring were commonly produced by white parents. Also, the variation of the coat colour pattern is mainly determined by alleles at the A locus where A^{wh} is the top allele determining white or tan colour of the fleece, as is reported in most of the white fleece breeds, even when face and legs are coloured [26] as was observed in some white Belle-Ile ewes. Black pattern in Belle-Ile sheep designates a general dark colour where different variants could be distinguished (red eye, dark grey, eye patch, etc.), as described in some other non-standardized breeds such as Icelandic sheep [2] or Corsican sheep [21].

Influence of A^{wh} on litter size has already been described in Icelandic sheep and other breeds (as reviewed by Jónmundsson and Adalsteinsson [18]), with a significant reduction in litter size estimated at 0.15 in white ewes compared with non-white. In our model, calculated on a rather small number of records, the effect of colour on litter size appeared to be significant only through its interaction with the class of maximum OR in the dam but trends are opposite in each class. The overall effect of A^{wh} on ovulation rate is more clear-cut with a depressive effect of 0.5. An interaction was identified between ewe colour and OR class of the dam but not between ewe colour and sire. As classification of the dam is not adjusted for colour effect, it is difficult to predict if the interaction would occur in case of previous adjustment.

As a control population of similar genetic background is not available in Belle-Ile sheep, as is the case with Merino or Icelandic sheep for example, and considering the interaction of colour pattern on ovulation rate expression as stated above, it is difficult to define a specific and sensitive criterion for typing pure-bred ewes in such a small inbred population without progeny records.

Unknown a few years ago, the traditional sheep population of Belle-Ile has to be considered as an endangered population. The small size of the population promotes inbreeding and genetic drift and restricts the possibility of investigations devoted to the confirmation of the existence of the putative gene. News method of pedigree analysis [13] could offer the possibility for such a validation.

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