Inbreeding and crossbreeding parameters for production and fertility traits in Holstein, Montbéliarde, and Normande cows

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ABSTRACT

Breed differences and nonadditive genetic effects for milk production traits, somatic cell score (SCS), conception rate (CR), and days to first service (DFS) were estimated for Holstein × Montbéliarde and Holstein × Normande crossbreds, using an animal model adapted from the French genetic evaluation and extended to across-breed analysis. Inbreeding and breed differences were estimated from all purebred recorded cows. Only records from 1,137 herds with Holstein × Montbéliarde crossbred cows and from 1,033 herds with Holstein × Normande crossbred cows were used to estimate crossbreeding parameters. In these herds, crossbred cows represented about 13% of the total number of recorded animals compared with <1% when all herds were considered. Compared with the Montbéliarde and Normande breeds, the Holstein breed was genetically superior for production [+951 kg and +2,444 kg for 305-d mature-equivalent (305ME) milk, +40 kg and +102 kg for 305ME fat, +17 kg and +54 kg for 305ME protein, respectively] and inferior for fertility traits (−12 and −9% for CR, respectively). Inbreeding depression caused loss of yield for production traits (from −32 to −41 kg of 305ME milk, −1.4 to −1.7 kg of 305ME fat, and −1.1 to −1.3 kg of 305ME protein per inbreeding percentage), a small increase in SCS (+0.001 to 0.006) and DFS (+0.12 d), and a decrease in CR (−0.27 to −0.44%). Favorable heterosis effects were found for all traits (+494 to 524 kg of 305ME milk, +21 to 22 kg of 305ME fat, +15 to 16 kg of 305ME protein, −0.05 to −0.04 SCS, +2 to 3% for CR, and −3 to 6 d of DFS), to such a point that F₁ crossbreds could compete with Holstein cows for milk production while having a better

fertility. However, recombination losses suggested that some F₁ heterosis was lost for backcross cows.

Key words: dairy crossbreeding, production trait, functional trait, nonadditive effect

INTRODUCTION

A large variety of dairy breeds exist in France, with 3 main breeds, Holstein (**HO**), Montbéliarde (**MO**), and Normande (**NO**), representing 65, 18, and 11%, respectively, of dairy cows (Institut de l'Élevage, 2013). With genetic selection first focused on yield traits, tremendous gains in milk, fat, and protein yields have been realized, especially in the Holstein breed, worldwide. But this genetic selection on yield, combined with intensification of herd management, has negatively affected fertility (Windig et al., 2005), udder health (Seegers et al., 2003), longevity (Hare et al., 2006), and inbreeding (Miglior et al., 2005; Danchin-Burge et al., 2012). Since 2001, the French total merit index has evolved to better account for functional traits, and it is hoped that genomic selection will reverse the past genetic trends (Ducrocq, 2010). However, the use of crossbred cows involving the Holstein breed may be an alternative solution (Weigel and Barlass, 2003; Sørensen et al., 2008) to combine good production and fitness. In previous studies, although first-generation crossbreds (F₁) tended to exhibit better functional traits and fat production than Holstein cows, the latter still had the highest milk production (Dechow et al., 2007; Heins and Hansen, 2012), and crossbreeding had less influence on production traits than on functional traits (Weigel, 2007). Indeed, expected heterosis effects for fertility of around 10% of the parental mean have been reported, compared with around 3% for production traits (Sørensen et al., 2008).

In France, most dairy cows are purebred animals. Consequently, nonadditive genetic effects expressed through heterosis, recombination loss, and inbreeding

Received May 19, 2014.

Accepted March 26, 2015.

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depression have not received much attention so far. French genetic evaluations currently consider data from different breeds separately, excluding information from crossbred cows. Although crossbreeding has remained marginal until recently, it has developed in the last 10 yr. Indeed, crossbred cows may be more profitable than cows from the parental pure breeds (McAllister, 2002; Heins et al., 2012). Therefore, it is desirable to estimate nonadditive genetic parameters, in particular heterosis and recombination effects, to assess such a benefit.

The objective of this study was to estimate the genetic differences between the Holstein, Montbéliarde, and Normande breeds as well as the effects of inbreeding, heterosis, and recombination loss for milk yield traits, SCS, and fertility traits.

MATERIALS AND METHODS

Data

Lactation records on 305-d mature-equivalent (**305ME**) milk yield, fat yield, fat content, protein yield, protein content and SCS, conception rate (**CR**) after AI, and days to first service (**DFS**) for lactation numbers 1 to 3 from 2000 to 2013 were extracted from the French National Genetic Information System. The French breeding law requires that AI are recorded and included in the national database. Hence, 100% of AI from cows with milk records (which represents 80% of the French dairy cattle) are recorded. Mature-equivalent production data were used to be consistent with the current national evaluation system, to homogenize variances across lactations, and to facilitate interpretation of within lactation number estimates of crossbreeding parameters. Mature-equivalent coefficients were constant across breeds and genotypes and depended only on parity. Following Poutous et al. (1981), multiplicative mature-equivalent factors were 1.3, 1.17, and 1.105 in first, second, and third lactations, respectively. Somatic cell count was log-transformed to SCS as follows: $SCS = \log_2 (SCC/100,000) + 3$. Conception rate was recorded as a repeated binary measure (conceived or not conceived after each of the first 3 AI). Days to first service was calculated as number of days from calving to first service. Breed proportion was computed for each cow and her parents from a total pedigree file of 173,025,861 animals of all cattle breeds existing in France. Cows with unknown parents and grandparents were removed. In this study, only cows for which the sum of breed proportions between Holstein and Montbéliarde and between Holstein and Normande breeds was equal to 1 were retained. Records from purebred, F_1 , and backcross cows were considered.

Four data sets were prepared. Only records from herd-year combinations with at least 10 cows were included. The first file included records from HO and MO purebred cows and the second file comprised records from HO and NO purebred cows. These 2 files were created to estimate inbreeding effects and breed differences. To analyze crossbreeding parameters, herd-year combinations with at least 3 crossbred cows were identified. The third and fourth files consisted of records of all HO and MO purebred cows and their crosses (HO $\times$ MO) on the one hand and HO and NO cows and their crosses (HO $\times$ NO) on the other hand, identified in these herds.

Inbreeding, Specific Heterosis, and Recombination Loss Coefficients

Inbreeding coefficients were computed with the Pedig software (Boichard, 2002) using the method described by VanRaden (1992), which adjusts inbreeding using an unknown-parent grouping strategy in 2 steps: first, inbreeding coefficients were computed for animals with at least 5 generations of ancestors known. Second, the inbreeding coefficients were computed for all animals, and means of inbreeding coefficients computed on the first step were assigned to unknown ancestors born during the same period.

Coefficients for heterosis (H) and recombination (R) effects were calculated as in Dechow et al. (2007):

$$H = 1 - \sum s_i d_i,$$

$$\text{and } R = 1 - \sum (s_i^2 + d_i^2)/2,$$

where s_i is the proportion of sire genes, and d_i is the proportion of dam genes from breed i .

Model

First, inbreeding and breed differences were jointly estimated from the first and second files. The use of all purebred cows guarantees a proper estimation of genetic trends in each breed and then a proper estimation of breed differences. The model was adapted from the French genetic evaluation:

$$Y_i = \Sigma \text{ fixed effects} + \beta_{1-2} \times \text{inbreeding[HO, MO, or NO]} + a_i + p_i + e_i,$$

and

$$V_{ij} = \Sigma \text{ fixed effects} + \beta_{1-2} \times \text{inbreeding[HO, MO, or NO]} + \beta_3 \times \text{inbreeding[embryo]} + \text{Bull}_j + a_i + p_i + e_i,$$

where Y_i = 305ME milk, fat, protein yields, fat content, protein content, SCS, or DFS for cow i ; V_{ij} = CR for cow i ; β_{1-2} = linear regression coefficients on inbreeding of the cow estimated separately for the different purebreds; β_3 = linear regression coefficient on inbreeding of the future progeny; $Bull_j$ = random effect of year-AI bull j depending on the breed of cow i ; a_i = additive genetic effect; p_i = permanent environmental effect; e_i = residual effect. Genetic groups were included in the additive genetic effect and were defined on the basis of breed and birth year. For production and SCS, fixed effects were herd-year and 3 effects nested within lactation number-year-region (i.e., age at calving, calving month, and dry period). For CR, fixed effects were herd-year, AI bull's breed, lactation number $\times$ DIM at insemination, month of AI-year-region, day of AI-year-region, AI technician-year, and year-lactation number. For DFS, fixed effects were calving age-lactation number, month of AI-year-region, and year-lactation number.

For production traits, the linear mixed model assumed heterogeneous residual variances (Robert-Granié et al., 1999) and constant variance ratios for the other random effects (i.e., constant heritability).

Breed differences and crossbreeding parameters were estimated from the third and fourth files. Again, the model was an extension of the French genetic evaluation model:

$$Y_i = \Sigma \text{ fixed effects} + \beta_4 \times H + \beta_5 \times R \\ + a_i + p_i + e_i,$$

and

$$V_{ij} = \Sigma \text{ fixed effects} + \beta_{1-2} \times \text{inbreeding}[\text{cow}] \\ + \beta_3 \times \text{inbreeding}[\text{embryo}] + \beta_4 \times H \\ + \beta_5 \times R + Bull_j + a_i + p_i + e_i,$$

where Y_i , V_{ij} , β_{1-2} , β_3 , $Bull_j$, a_i , p_i , and e_i are the same as defined previously; β_4 and β_5 are the regression coefficients on heterosis (H) and recombination loss (R), respectively, estimated over all lactations (i.e., assuming that the effects are constant for each lactation). No additional regression on breed composition was added, because it was already accounted for in the additive effect and unknown parent groups. Indeed, as in VanRaden et al. (2007), unknown parent groups in the animal model were separated according to breed, pedigree path (dams of cows, sires of cows and parents of sires), origin (French or foreign), and birth year. Therefore, the model allowed a proper estimation of genetic trends in each breed, and breed differences could be computed

as differences between average additive genetic effects estimated for each breed.

The data sets were analyzed using Genokit, an in-house genetic evaluation software (V. Ducrocq, Institut National de la Recherche Agronomique, Jouy en Josas, France; personal communication). Breed differences were estimated as the difference between breeding values of the HO and MO (and HO and NO) herdmate cows. Breed differences estimated from the first file (and the second file) were compared with breed differences estimated from the third (and the fourth) file to validate the estimations of crossbreeding parameters. Phenotypic differences were also those observed for the same cows.

For simplicity, a lower bound of crossbreeding parameters standard errors were obtained with a simplified homoskedastic model with the same fixed effects and the effect of Holstein genes percentage but without random effects.

RESULTS

Raw Performance

Only herds with at least 3 crossbred cows per herd-year were considered for the crossbreeding analysis. As a result, records from 1,137 herds with HO $\times$ MO crossbred cows and from 1,033 herds with HO $\times$ NO cows were analyzed. Records represented about 50% of all dairy crossbred animals, although they represented only a very small proportion of the total French HO, MO, and NO cows (Tables 1 and 2). Means for production and fertility traits of purebred cows in these herds were close to the mean population of all purebred cows. More crossbred cows were recorded in the HO $\times$ NO population than in the HO $\times$ MO population (especially 3/4 NO cows compared with 3/4 MO cows; Table 2). Around 85% of F₁ HO $\times$ MO crossbred cows were from an HO dam and an MO sire, whereas around 69% of F₁ HO $\times$ NO crossbred cows were from an HO dam and an NO sire. In both files, fewer than 100 cows were from an MO $\times$ HO (or NO $\times$ HO) dam and an HO sire. Average 305ME milk, fat, and protein yields increased when the proportion of HO genes increased from 0 to 100%, except for MO backcrossed cows, which produced less milk than the others (Table 2). The HO $\times$ MO and HO $\times$ NO F₁ crossbred cows had lower 305ME milk production than MO $\times$ HO and NO $\times$ HO F₁ crossbred cows, respectively. On average, F₁ crossbreds in the HO $\times$ MO data set and F₁ crossbreds in the HO $\times$ NO data set had 305-d milk production 721 and 1,378 kg lower than that of purebred HO cows, respectively. Normande cows had the highest fat and protein contents (4.33 and 3.47%, respectively), where-

as MO cows had slightly lower fat content but higher protein content than HO cows (3.93 vs. 4.00% and 3.30 vs. 3.20%, respectively). However, MO cows recorded in herds with crossbreeding had a higher fat content than HO cows recorded in herds with crossbreeding (3.99 vs. 3.94%). Montbéliarde cows had the lowest SCS (3.21) and NO cows had the largest SCS (3.78). All HO $\times$ MO crossbred cows had lower SCS (3.53 for all 3/4 HO cows, 3.37 for all F₁, and 3.40 for all 3/4 MO cows) than HO cows (3.62). However, HO $\times$ NO crossbred cows had a higher SCS (3.65 for all 3/4 HO, 3.68 for all F₁ cows, and 3.82 for all 3/4 NO cows). Both MO and NO cows had a much better CR than HO cows (51, 46, and 38%, respectively). However, HO cows recorded in herds with crossbreeding had a slightly higher CR than their average population (41% in the HO $\times$ MO file and 40% in the HO $\times$ NO file). The F₁ crossbred cows had a CR close to the corresponding MO or NO purebreds (52% for HO $\times$ MO and 48% for HO $\times$ NO). These performances suggest an important heterosis effect. Average DFS was 16 d shorter for MO cows and 14 d shorter for NO cows compared with HO cows. Compared with purebred cows, DFS was intermediate for crossbred cows in the 2 populations.

Inbreeding Effects

Figure 1a-c represents the evolution of the average inbreeding level over time in France for HO, MO, and NO cows and their ancestors, excluding or including unknown ancestors when computing inbreeding coefficients. Each plot shows that excluding unknown ancestors led to an underestimation of the inbreeding level. Since 1990, inbreeding has dramatically increased in the 3 breeds up to 4.5 to 5% for cows born in 2009.

Estimates of inbreeding depression were unfavorable for all traits (Table 3). A 1% increase in inbreeding had a greater effect on milk, fat, and protein yields and a lesser effect on CR for HO cows than for MO or NO cows. However, when expressed as percentage of the phenotypic mean, inbreeding depression affected all 3 breeds in the same way. Moreover, it was higher for CR (from 0.7 to 0.9% of the mean) than for milk yield (0.4% of the mean), and was negligible for fat and protein contents, except for fat content in the Normande breed. Inbreeding had a small effect on SCS (0.2% of the mean) and on DFS (0.1% of the mean).

Crossbreeding Parameters

Differences in breed estimates compared with the HO breed were larger for the NO breed than for the MO breed for production traits (Table 4). Holstein cows were superior for yields but inferior for fat and protein contents. Estimated breed differences sometimes greatly differed from the raw phenotypic means. For example, in the purebred file with HO and MO cows, the phenotypic difference between HO and MO cows was 1,600 kg for milk production when the estimated genetic difference was only 951 kg. This is explained by the unequal distribution of breeds in the different environments. For instance, MO cows are in higher proportion in more difficult and lower-producing environments. Raw differences between breeds include differences between herds and production systems, whereas estimated breed differences are obtained within herd-year and expected to be unbiased. Breed difference estimates for SCS were favorable for MO cows compared with HO cows (−0.2 SCS) but unfavorable for NO cows compared with HO cows (+0.4 SCS; Table 4). Both MO and NO cows were

Table 1. Number of cows, lactation records, and AI records, and means of production and fertility traits in 2 sub-populations of purebred cows¹

Item ²	HO and MO purebreds		HO and NO purebreds	
	HO	MO	HO	NO
No. of cows	6,617,000	1,047,548	6,617,000	1,000,065
No. of lactations	13,786,064	2,190,981	13,786,064	2,082,599
Milk (kg)	9,376	7,776	9,376	6,912
Fat (kg)	373	305	373	299
Protein (kg)	300	257	300	240
Fat content (%)	4.00	3.93	4.00	4.33
Protein content (%)	3.20	3.30	3.20	3.47
SCS	3.56	3.21	3.56	3.78
No. of AI	21,548,401	3,125,578	21,548,401	3,125,578
CR (%)	38	51	38	46
DFS (d)	92	78	92	80

¹HO = Holstein, MO = Montbéliarde, NO = Normande.

²CR = conception rate; DFS = days to first service.

Table 2. Number of cows, lactation records, and AI records, and means of production and fertility traits in the 2 sub-populations of cows recorded in herds with at least 3 crossbred cows

Item ¹	HO × MO file ²								HO × NO file ³							
	HO	3/4 HOa	3/4 HO _b	F _{1a}	F _{1b}	3/4 MOa	3/4 MO _b	MO	HO	3/4 HOc	3/4 HO _d	F _{1c}	F _{1d}	3/4 NOc	3/4 NO _d	NO
No. of cows	36,842	880	409	4,212	732	706	98	9,023	32,166	530	445	3,557	1,599	1,300	83	16,061
No. of lactations	50,270	1,361	653	7,930	1,246	1,206	172	13,213	43,568	779	643	6,574	2,594	2,272	131	23,423
Milk (kg)	9,405	9,070	9,103	8,595	9,214	7,732	8,283	7,968	9,372	8,801	8,864	7,837	8,300	6,898	7,345	6,774
Fat (kg)	368	359	355	349	361	310	329	317	368	349	349	326	335	290	306	287
Protein (kg)	298	288	290	278	297	250	268	263	299	283	286	261	272	233	244	234
Fat content (%)	3.94	3.98	3.93	4.08	3.95	4.03	3.99	3.99	3.96	4.00	3.97	4.18	4.06	4.22	4.18	4.25
Protein content (%)	3.23	3.18	3.19	3.24	3.23	3.24	3.24	3.30	3.20	3.22	3.23	3.33	3.29	3.38	3.32	3.46
SCS	3.62	3.47	3.65	3.35	3.46	3.40	3.35	3.32	3.59	3.66	3.64	3.72	3.58	3.83	3.62	3.86
No. of AI	126,851	2,287	1,179	12,560	2,036	2,001	329	28,659	112,226	1,553	1,114	10,655	4,013	3,514	221	47,589
CR (%)	41	45	44	52	48	52	47	51	40	44	45	48	48	46	48	48
DFS (d)	96	90	89	84	84	83	77	80	96	91	92	83	85	83	82	82

¹CR = conception rate; DFS = days to first service.
²HO = Holstein; MO = Montbéliarde; 3/4 HOa = (HO × MO) dam × HO sire; 3/4 HO_b = (MO × HO) dam × HO sire; F_{1a} = HO dam × MO sire; F_{1b} = MO dam × HO sire; 3/4 MOa = (HO × MO) dam × MO sire; 3/4 MO_b = (MO × HO) dam × MO sire.
³NO = Normande; 3/4 HOc = (HO × NO) dam × HO sire; 3/4 HO_d = (NO × HO) dam × HO sire; F_{1c} = HO dam × NO sire; F_{1d} = NO dam × HO sire; 3/4 NOc = (HO × NO) dam × NO sire; 3/4 NO_d = (NO × HO) dam × NO sire.

Figure 1. Inbreeding trend computed assuming unknown parents unrelated and non-inbred (triangles) or assuming unknown parents as inbred as their contemporaries and related accordingly (diamonds) for (a) Holstein, (b) Montbéliarde, and (c) Normande cows and their ancestors.

largely superior to HO cows for CR (11 and 9%, respectively; Table 4). Breed differences estimated from HO and MO or NO cows in herds with at least 3 crossbred cows presented some differences with those estimated from all HO, MO, and NO purebred cows, showing that the selection policy was not exactly the same between

Table 3. Effect of 1% increase of inbreeding on 305-d milk, fat, and protein yields; fat and protein contents; SCS; conception rate (CR¹); and days to first service (DFS) in absolute terms and expressed as percentage of the phenotypic mean (in parentheses) by breed

Trait	Breed		
	Holstein	Montbéliarde	Normande
Milk (kg)	-41 (0.4)	-35 (0.4)	-32 (0.4)
Fat (kg)	-1.7 (0.4)	-1.4 (0.4)	-1.4 (0.5)
Protein (kg)	-1.3 (0.4)	-1.1 (0.4)	-1.3 (0.5)
Fat content (%)	-0.0003 (0.008)	-0.00004 (0.001)	-0.001 (0.02)
Protein content (%)	0.0002 (0.006)	0.0002 (0.006)	-0.0001 (0.003)
SCS	0.006 (0.2)	0.006 (0.2)	0.001 (0.3)
CR (%)	-0.27 (0.7)	-0.44 (0.9)	-0.38 (0.8)
DFS (d)	0.12 (0.1)	0.12 (0.1)	0.12 (0.1)

¹CR was recorded as a repeated binary measure (conceived or not conceived after each of the first 3 AI).

these 2 types of herds. Nevertheless, the general picture and the ranking between breeds were the same.

Heterosis estimates for production traits were favorable and similar between HO × MO and HO × NO crossbred cows (524 vs. 494 kg for 305ME milk, 22 vs. 21 kg for 305ME fat, and 16 vs. 15 kg for 305ME protein, respectively; Table 5). They represented around 6% of the parent breed means (computed from Table 2). Therefore, with the heterosis effect, F₁ HO × MO crossbred cows reached the same genetic level as HO cows for production traits. A favorable heterosis effect for fat content, representing 6% of the parent breeds mean, and an unfavorable but nonsignificant recombination loss (-0.023%) were found in HO × MO crossbreds. However, a smaller heterosis effect (0.006%) but a higher recombination loss (-0.076%) were found for fat content for HO × NO crossbreds. For both HO × MO and HO × NO crossbred cows, a very small heterosis effect was found for protein content (0.001 and -0.005% respectively). Recombination losses for protein content were larger than the heterosis effect (-0.025 and -0.058%, respectively). However, Table 5 shows that crossbreeding effects had limited effects on contents. Heterosis estimates for SCS were very small

(-0.05 SCS for HO × MO crossbreds and -0.04 SCS for HO × NO crossbreds). For SCS, a larger recombination loss was found for HO × MO crossbreds (+0.20 SCS) than for HO × NO crossbreds (+0.08 SCS). However, crossbreeding effects had limited effect on SCS (Table 5). For fertility traits, heterosis estimates were favorable but smaller than anticipated (Table 5). Heterosis for CR represented 6.5% (5%) of the parent breed mean in HO × MO (HO × NO) crossbred cows even though the average CR of F₁ cows was 52% (48%). Recombination loss estimates were unfavorable (-5%, in absolute value, of CR for HO × MO crossbreds and -4% of CR for HO × NO crossbreds). Therefore, combined crossbreeding parameters were close to zero for 3/4 cows, performances of which were close to expectations based on breed differences only, although the raw phenotypic performance suggested more favorable recombination loss for 3/4 HO cows. Moreover, the phenotypic average CR of 3/4 MO was similar to that of MO cows. For DFS, even though MO cows were genetically superior to NO and HO purebred cows (-16 and -13 d, respectively), heterosis was greater in HO × NO crossbred cows than in HO × MO cows (3 vs. 7% of the parent breeds mean, respectively; Table 5). Recombination

Table 4. Genetic breed differences estimated from a data set with all purebred cows compared with those from a data set including purebred and crossbred herdmatе cows¹

Genetic difference	Files with only purebreds		HO×MO file	HO×NO file
	HO-MO	HO-NO	HO-MO	HO-NO
Milk (kg)	951	2,444	1,153	2,026
Fat (kg)	40	102	37	71
Protein (kg)	17	54	28	53
Fat content (%)	-0.03	-0.27	-0.11	-0.27
Protein content (%)	-0.05	-0.11	-0.12	-0.24
SCS	0.33	-0.45	0.30	-0.43
Conception rate (%)	-12	-9	-13	-13
Days to first service (d)	13	11	16	8

¹HO = Holstein, MO = Montbéliarde, NO = Normande.

Table 5. Heterosis and recombination loss estimates (SE) for 305-d milk, fat, and protein yields, conception rate (CR¹), and days to first service (DFS) for the Holstein × Montbéliarde (HO × MO) and Holstein × Normande (HO × NO) sub-populations

Estimate	Milk (kg)	Fat (kg)	Protein (kg)	Fat content (%)	Protein content (%)	SCS	CR (%)	DFS (d)
Heterosis								
HO × MO	524 (28)	22 (1.1)	16 (0.9)	0.023 (0.008)	0.001 (0.004)	−0.05 (0.026)	3 (0.7)	−3 (0.7)
HO × NO	494 (20)	21 (0.8)	15 (0.6)	0.006 (0.006)	−0.005 (0.003)	−0.04 (0.02)	2 (0.6)	−6 (1.8)
Recombination loss								
HO × MO	−183 (129)	11 (5.2)	−7 (4.0)	−0.023 (0.036)	−0.025 (0.017)	0.20 (0.12)	−5 (2.8)	0.3 (3.1)
HO × NO	−128 (113)	−6 (4.6)	−3 (3.6)	−0.076 (0.033)	−0.058 (0.016)	0.08 (0.11)	−4 (2.7)	−4 (4.6)

¹CR was recorded as a repeated binary measure (conceived or not conceived after each of the first 3 AI).

loss for DFS was unfavorable but very small for HO × MO cows (+0.3 d), whereas it was favorable for HO × NO cows (−4 d).

DISCUSSION

In this study, we aimed to estimate additive and nonadditive genetic effects in the 3 main French breeds for production and fertility traits. Although breeds are currently evaluated separately in France, our study estimated breed difference and inbreeding and crossbreeding effects in 2 crossbred sub-populations, HO × MO and HO × NO. For a proper estimation of inbreeding effects, all the national purebred records were used. The inclusion of all purebred data in a single model also guaranteed a fair assessment of the genetic merit of parents, which is necessary to avoid biased estimates of breed differences. A threshold of 3 crossbred cows per herd-year combination was defined to select herds in data sets 3 and 4. This figure may appear quite low but crossbred cows represented 13% of the cows in these herds and 40% of all crossbred animals. It should be kept in mind that French herds had and still have a limited size, and requiring more crossbreds per herd would have reduced the population studied by 40%. The inclusion of only cows recorded in these herds with at least 3 crossbred cows in a single model also guaranteed a fair assessment of crossbreeding parameters, if the breed differences estimated from these records are valid. The number of F₁ crossbred cows was small compared with the number of purebreds but large enough to allow a proper estimation of heterosis effect in both populations. However, in the HO × MO population, 85% of the F₁ crossbreds had an HO dam and an MO sire. Therefore, the heterosis estimated in this population reflected both genotype effect and mating direction. Due to the small number of 3/4 crossbred cows, especially in the HO × MO population, estimates of recombination loss effects were not as accurate. There was also an imbalance between the number of 3/4 MO and 3/4 HO crossbreds in the HO × MO population. In both populations, the number of 3/4 MO (NO) cows

with an F₁ dam born from an MO (NO) dam and an HO sire was quite small compared with 3/4 MO (NO) cows with an F₁ dam born from an HO dam and an MO (NO) sire. This is in agreement with the previous observation on F₁ crossbred cows. Standard errors of estimates indicated that recombination losses were never significant in this study, although they had quite large values and were consistent across breeds, suggesting unfavorable effects.

The use of mature-equivalent production increased means of production compared with other studies on actual production, especially for first and second lactations. Therefore, it increased estimates of breed differences and absolute values of inbreeding and crossbreeding parameters. However, because coefficients were the same across breeds, they did not influence estimates of breed differences and crossbreeding parameters expressed relative to the mean. Production level of HO cows was largely superior to that of the 2 other purebred cows, whereas fertility level was largely inferior, as indicated in Barbat et al. (2010). However, HO cows recorded in herds with crossbred cows had better raw fertility than the average population (41 vs. 38%). This might be at least partially explained by the use of MO bulls, with better male fertility than HO bulls (Seegers et al., 2001). Indeed, in herds with crossbreeding, 7.5% of AI on HO cows were with an MO bull compared with only 0.3% in purebred Holstein herds. Difference of DFS between the respective purebreds in the 2 data sets was around 15 d, even when cows of the 2 different breeds were herdmates. Such a difference when the herd environment is the same is clear evidence that overall breed difference in DFS is real and not just the result of farmers' decisions. As in a previous national report on SCS (Rupp et al., 2000), NO cows had the highest SCS compared with HO and MO cows, although they have the lowest milk production. Hence, NO cows seemed to be more susceptible to SCS than HO or MO cows. Except for SCS in the HO × NO sub-population, we found differences between F₁ HO × MO cows or F₁ HO × NO cows and HO purebred cows similar to those reported by Heins and Hansen (2012) for yields and

DFS. This may suggest that independently from the environment, F_1 crossbreds performed for these traits nearly the same compared with HO purebreds.

In a previous study of genetic diversity of French dairy cattle, Danchin-Burge et al. (2012) found lower inbreeding levels, close to 4%. Miglior and Burnside (1995) reported that assuming that unknown ancestors are unrelated led to an underestimation of the inbreeding level. Hence, not surprisingly, accounting for relatedness of unknown ancestors in our study led to a higher level of inbreeding of cows born in 2010, averaging 4.5 to 5%. However, the greatest impact of inbreeding in dairy cattle is assumed to be on traits expressed early in life (Adamec et al., 2006; Mc Parland et al., 2007). The cows in the study are those that survived as an embryo, that were born alive (rather than stillborn), that survived as a heifer (rather than dying or being sterile), and that survived adequate days postcalving to enter milk recording. Therefore, for these selected cows, inbreeding was likely to be underestimated. Inbreeding depression was observed for all traits and was similar across breeds when expressed as a percentage of the phenotypic mean, except for fat content in the NO breed. Generally, we found a larger effect of inbreeding for production traits (more than -30 kg for milk, -1.4 kg for fat, and -1.1 kg for protein) than in Miglior et al. (1995a) or Croquet et al. (2006) where a 1% increase in inbreeding caused a loss of 20 to 25 kg for milk, 0.90 to 0.96 for fat, and 0.69 to 0.79 for protein. This might be explained by the use of mature-equivalent production, which inflates the estimates accordingly. However, when inbreeding is expressed as percentage of the mean, Miglior et al. (1995b) found the same inbreeding effect on yields, but found an increase of fat and protein content for each 1% increase in inbreeding compared with our results. However, the effect of inbreeding on contents was, as in our study, very small, which may be related to the high heritability of these traits. Inbreeding had a small effect on SCS, again as in Miglior et al. (1995a) or Croquet et al. (2006). Despite a low value of inbreeding depression of 0.005 for SCS, Croquet et al. (2006) found that this effect was highly significant. Wall et al. (2005) found that 1% inbreeding caused a 0.2% increase in the SCS phenotypic mean, which is very close to our finding (a 0.1% increase). However, the inbreeding effect might be nonlinear, with a positive effect at low inbreeding level and a negative effect at high inbreeding level (Wall et al., 2005; Mc Parland et al., 2007).

Estimations of genetic breed differences for production and fertility traits were consistent with the average raw observations. Penasa et al. (2010) estimated breed differences between MO and HO breeds of 731 kg for 305ME milk, 32.9 kg for 305ME fat, and 18.2 kg for

305ME protein. These differences are lower, except for protein yield, than those reported here, possibly because of the use of mature-equivalent production in this study. Regarding SCS, NO were genetically inferior to HO and HO were genetically inferior to MO. This confirmed that NO cows are more susceptible to sub-clinical mastitis than HO cows, whereas HO cows are more susceptible than MO cows. Genetic superiority of MO and NO compared with HO cows for CR explained almost all the observed phenotypic differences. Hence, when crossbreeding effects are neglected, MO additive effects allow a 6% gain of CR in F_1 crossbred cows compared with HO. Breed differences estimated in the whole population or in the sample of herds with crossbred cows were similar, showing that this reduced sample of herd is valid for crossbreeding parameters estimation.

Heterosis estimates over all lactations were favorable and close to the literature results for milk production (i.e., 6% of parental mean for production traits, as reported in Sørensen et al., 2008). Crossbreeding effects were important for production traits but we found a negligible heterosis effect for contents, except for fat content in the HO $\times$ MO population. The small estimates of heterosis and recombination loss effects for contents could be related to the high heritability of these traits. De Haas et al. (2013) and Freyer et al. (2008) found similar results. The higher estimates of crossbreeding parameters on fat content in the HO $\times$ MO population might be related to the large heterosis effect estimated for fat yield in this population. For SCS, we estimated a small favorable heterosis effect, as in Dechow et al. (2007). However, VanRaden and Sanders (2003) found a small but unfavorable (0.016) heterosis. The small magnitude of nonadditive effects (inbreeding and crossbreeding) for SCS is consistent with the small reported dominance variance of the trait (Miglior et al., 1995a). Relatively small heterosis effects were estimated for reproduction traits: 6.5% (4.5%) of HO $\times$ MO (HO $\times$ NO) parental mean for CR and 3.4% (6.7%) for DFS. These results differ from the estimation of 10% heterosis for daughter pregnancy rate indicated by VanRaden et al. (2004). However, in a Danish experiment, Sørensen et al. (2008) also reported a small heterosis effect for traits related to pregnancy rate. Our estimates of heterosis on DFS are close to those reported by Sørensen et al. (2008) and Wall et al. (2005).

We found negative recombination estimates for all traits but their standard errors were always large. Consequently, estimates, although always unfavorable and consistent across breeds, were not significantly different from zero. In the French context, most crossbred cows probably result from situations where pure HO herds

were being upgraded to pure MO herds or from pure NO herds being upgraded to pure HO herds. Therefore, the reduced number of 3/4 cows added to an unbalanced number of 3/4 HO cows compared with 3/4 MO (NO) cows might explain our estimates of recombination loss. In many countries, 3-breed rotational crossbreeding is often recommended. Unfortunately, our data were not adequate to study such a crossbreeding plan here. Admittedly, our estimation of crossbreeding parameters using only F_1 and backcrosses is not adapted to such study.

Effects of inbreeding and crossbreeding found in this study could affect cow and farm profitability. In Belgium, Croquet et al. (2006) found that a 1% increase in inbreeding cost €6.13 per cow based on their total economic index. In contrast, crossbreeding seems to affect positively cow profitability. Indeed, Heins et al. (2012) found that Montbéliarde $\times$ Holstein cows and Scandinavian Red $\times$ Holstein cows had a higher profit per day than Holstein cows (+\$0.22 and +\$0.15 respectively). However, French dairy farms are different from US farms. A study of cow and farm profitability of crossbreeding depending on the mating system and the system of production is planned but is out of the scope of this paper.

CONCLUSIONS

Crossbreeding between the main 3 French dairy cattle breeds is currently limited (0.25% in our data set), but a joint analysis of national data sets of production and functional traits for all purebred cows and for herd-mate purebred and crossbred cows allowed estimation of actual breed genetic differences, as well as inbreeding and crossbreeding parameters. Many of the parameter estimates were in line with previous reports. Overall, HO $\times$ MO F_1 crossbreds were found to be genetically almost as productive as purebred HO cows (with a reduction of only 55 kg in milk production but with similar fat and protein yields) while being more fertile (+7% of CR). The HO $\times$ NO F_1 cows showed similar characteristics for each trait but to a lesser extent. Heterosis effects on contents were small, but because of the breed superiority of both MO and NO for these traits, F_1 crossbreds had higher fat and protein contents than HO cows. Crossbreeding with the MO breed favored a decrease of SCS, whereas crossbreeding with the NO breed tended to increase SCS. Recombination loss estimates were all in the unfavorable direction but because of the limited number of backcrossed cows, these estimates were never significantly different from zero. For rotational crossbreeding (not studied here), these results suggest that the choice of breeds involved

and their sequence must be investigated to maximize heterosis effects and to minimize recombination losses.

ACKNOWLEDGMENTS

This study was funded by PASS'SAS (Roulans, France). We are thankful to the Centre de Traitement de l'Information Génétique of INRA for providing the data used in this study and to the French Livestock Institute (Paris, France) for helping us to access these data. We also acknowledge the numerous comments of the anonymous reviewers that helped to improve this paper.

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