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1         **Genetic parameters of litter weight, an alternative criterion to prolificacy and pre-weaning**  
2                                   **weight for selection of French meat sheep**

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## ABSTRACT

Weight of lambs produced per ewe is an important economic-related trait for French meat sheep farmers. Consequently, genetic improvement of their ewes is based on selecting maternal traits using a global index, called MAT, which combines estimated breeding values for litter size at lambing (LS), weight at 30 days of age (W30D) and viability over the same period. The frame of this study is to compare the official approach to genetic evaluation of maternal traits which combine several estimated breeding values with a direct genetic evaluation of a proxy trait of the farmer's objective. The weight of lambs produced per ewe and per lambing was chosen as this proxy of meat production potential of ewes. In a first step, we estimated the genetic parameters of this alternative criterion, the litter weight (LW), which is the sum of the W30Ds of lambs of the same litter. In a second step, we compared these parameters with those of LS, W30D and MAT, which are routinely used. Datasets comprising 2006-2018 records of 190,883 and 271,963 litters of the Ile de France (IF) and Blanche du Massif Central (BMC) breeds respectively, were analysed. The genetic evaluations were performed using Asreml software according to BLUP animal models, which were the closest to the models used in routine evaluation. Two models are presented: a two-trait model LS and W30D and a two-trait model LS and LW. For LS and LW, records are linked to ewes. For W30D, both direct and maternal effects were considered. Direct animal variance ( $\sigma^2_{a\_LW} = 28.02$  for IF and  $\sigma^2_{a\_LW} = 16.55$  for BMC) and heritability ( $h^2_{a\_LW} = 0.06$  for IF and  $h^2_{a\_LW} = 0.04$  for BMC) of LW suggest it is possible to select based on this trait while simultaneously improving LS ( $rg_{a\_LS/a\_LW} = 0.78$  for IF and  $rg_{a\_LS/a\_LW} = 0.67$  for BMC). Moreover, the genetic progress curves of MAT and LW indicate that the selection based on MAT gave a positive correlated response on LW. Highly correlations between MAT and LW breeding values were estimated ( $rg = 0.85$  for IF and BMC breeds).

43            *Keywords: meat sheep, selection objective, genetic evaluation, prolificacy, weight at 30 days of*  
44   *age, litter weight*

45           **1. Introduction**

46           French meat sheep breeders want to simultaneously improve both maternal and meat traits  
47 (Ménissier and Bouix, 1992). To reach this goal, synthetic indexes are available combining the  
48 predicted genetic values for traits by weighting them according to their economic importance. Based on  
49 a bio-economic model, Cheype et al. (2013) derived the weight of traits and showed that maternal traits  
50 play a major role in the selection objective for meat sheep. For example, in the Blanche du Massif  
51 Central breed, based on economics, the selection objective is composed of 71% maternal traits and  
52 29% meat traits. Among the maternal traits taken into account, 21% are attributed to prolificacy, 29%  
53 to the combination of pre-weaning weight and lamb viability and 21% to fertility. In France, the  
54 genetic evaluation of maternal traits is based on data (pedigrees, litter information and lamb weight)  
55 collected from the flock. Two maternal traits are under selection: litter size at lambing (LS) and  
56 maternal abilities, which combine weight at 30 days of age (W30D) and viability of lambs over the  
57 same period. First, estimated breeding values (EBVs) are predicted using a BLUP animal model.  
58 Breeding values for LS are estimated based on a two-trait model that considers LS after natural oestrus  
59 and LS after induced oestrus, as two different but genetically linked traits. For W30D and viability,  
60 both maternal and direct genetic effects are evaluated (Tiphine et al., 2011). Second, two indexes are  
61 computed: an "LS" index that mixes EBVs for LS after natural and induced oestrus, and a "maternal  
62 ability" index which is a linear combination of direct and maternal EBVs of W30D and of viability.  
63 Both "LS" and "maternal ability" indexes are provided to breeders. Third, a synthetic maternal index  
64 named MAT is computed using a linear combination of the "LS" and the "maternal ability" indexes  
65 according to coefficients based on the breeding goal defined by the breeder societies. In this study, we  
66 have estimated EBV\_LS and EBV\_W30D that were combined to compute EBV\_ MAT. The  
67 relationships between the elementary components are complex, particularly those between the dam and  
68 her lambs from birth to weaning (Petit and Liénard, 1988; Ménissier, 1976); therefore we have

69 considered an alternative criterion in line with one farmer's objective: the weight of lambs produced  
70 per ewe. This new criterion is the litter weight (LW), and is defined as the sum of W30Ds of the lambs  
71 of the same litter. Although it is not the net margin resulting of each lambing, it can be considered as a  
72 proxy trait to meat production potential of ewes. The assumption is that the use of the EBV\_ LW could  
73 be a selection criterion as is the use of a linear combination of the EBV of elementary components. For  
74 any new selection criterion, the first step is the estimation of its genetic parameters (Vanimisetti et al.,  
75 2007), this is the purpose of this study for LW. Research on such an alternative criterion has already  
76 been conducted but with lamb weights at weaning. Duguma et al. (2002) suggested combining the  
77 number of lambs weaned and the total weight of lambs weaned per ewe per year, while Bromley et al.  
78 (2001) suggested using LW at weaning alone and reported the heritability of this criterion to range  
79 from 0.02 to 0.11. The objective of the present study was to estimate the genetic parameters of such a  
80 criterion adapted to the French context of the sheep on-farm recording where individual lamb weight is  
81 not recorded at weaning but at 30 days of age. At this age, lambs have only been fed by their mother,  
82 W30D thus allows an effective estimation of maternal traits with no bias related to the transition to  
83 solid food.

84

## 85 **2. Material and methods**

### 86 Description of the dataset

87 This study was based on two French meat sheep breeds, Ile de France (IF) and Blanche du Massif  
88 Central (BMC). The first breed is a national breed mainly raised indoors throughout France, while the  
89 second is a local breed mainly raised outdoors and is common in the central part of France. Records  
90 from 2006 to 2018 were extracted from the official national genetic database for analysis. Records with  
91 outliers or missing data were removed from the dataset as were categories with low numbers such as  
92 adopted or artificially suckled lambs. After data editing, around 90% of records were retained. The

93 final dataset contains litter records of 73,435 IF and 81,733 BMC ewes and data on their 302,947 and  
94 397,362 lambs, respectively (Table 1). The average number of litters per ewe was 2.6 for IF ewes and  
95 3.3 for BMC ewes with a mean number of lambs born per lambing of 1.6 and 1.5, respectively. For  
96 lambs, the percentage of mortality between birth and 30 days old was slightly higher in BMC sheep  
97 flocks (13.2%). Information was available on the sire of half the IF lambs while the percentage was  
98 33% for BMC breed.

99

#### 100 Variables analysed

101 Genetic parameters were estimated for three traits: litter size at lambing (LS), weight of individual  
102 lamb at 30 days of age (W30D) and litter weight (LW) which is the sum of the W30Ds of lambs of the  
103 same litter. Viability was not included in this study as it has been shown that the correlation between  
104 MAT constructed with or without viability is high:  $r = 0.99$  (Tortereau, unpublished data). The number  
105 of lambs born (alive + stillborn) as well as W30D were directly available from the database. LW was  
106 calculated by summing the W30D of the lambs corrected for the sex for each litter. According to  
107 results of a pre-run univariate analysis made from the dataset of this study (not published and not  
108 shown), the W30D of female lambs was 0.6 kg higher. As stillborn lambs and lambs that died before  
109 30 days of age were included (W30D = 0), LW could be equal to zero. Litters with lambs of extreme  
110 weight i.e.  $\pm 2.5$  kg standard deviation (W30D < 2 kg and W30D > 50 kg), except 0, were discarded  
111 for the analysis of LS, W30D and LW, i.e. 1.6% of the weights for IF and 1.8% for BMC. The  
112 synthetic maternal index (MAT) was computed as follows:

$$113 \quad \text{MAT IF} = 1/2 * \text{EBV\_LS} + 1/2 * \text{EBV\_W30D}$$

$$114 \quad \quad \quad = 1/2 * \text{EBV\_LS} + 1/2 * (\text{EBV\_aW30D} + \text{EBV\_mW30D})$$

$$115 \quad \text{MAT BMC} = 2/3 * \text{EBV\_LS} + 1/3 * \text{EBV\_W30D}$$

$$116 \quad \quad \quad = 2/3 * \text{EBV\_LS} + 1/3 * (\text{EBV\_aW30D} + \text{EBV\_mW30D})$$

117 where 'a' denotes direct additive genetic effect and 'm' maternal additive genetic effect

118

119 Data analysis

120 Each breed was analysed independently as they are not connected. The models used to estimate the  
121 genetic parameters were close to the models used in the official genetic evaluation.

122 In the first exploratory step, LS was analysed with a bi-variate BLUP animal model considering LS  
123 after natural and induced oestrus as two different traits. However, since the genetic correlation between  
124 these two LS traits was high ( $r_g = 0.87$  for IF and  $r_g = 0.77$  for BMC, data not shown) as reported in  
125 the literature (Janssens et al., 2004), in subsequent models, the type of oestrus was considered as a  
126 fixed effect to limit computation time.

127 A multiple-trait model LS/W30D/LW was used to estimate the genetic correlations between LW and  
128 the elementary components. Unfortunately, in the case of a ewe with a litter of a single lamb, W30D  
129 and LW have the same value, which would create confusion in the model. We were consequently  
130 forced to consider two multiple-trait models to estimate the genetic parameters: a two-trait model  
131 LS/W30D and a two-trait model LS/LW.

132 In the LS/W30D model, performances were designed using a direct animal effect for LS where the  
133 records referred to the ewe, and direct and maternal effects for W30D where the records referred to the  
134 lambs. For LS, three additional random effects were taken into account: a permanent environmental  
135 effect, a herd-year-season (HYS) effect, and a residual effect. Four fixed effects were also included in  
136 the model: the type of oestrus, the type of mating, the physiological status of the ewe, and the month of  
137 birth of the ewe (Table 2). For the W30D of each lamb, the direct genetic effect reflects the growth  
138 capacity of the lamb while the maternal genetic effect reflects the general abilities of the ewe, in  
139 particular milk production and maternal behavior. In addition, a permanent environmental effect of the  
140 dam, a litter effect, a HYS effect, and a residual effect were included as random effects in the model.



141 Three fixed effects were used: the physiological status of the dam, the overall status of the lamb, and  
142 the combination of birth type and rearing methods of the lamb (Table 2). In the LS/LW model, the  
143 effects fitted of LS were the same as those fitted for LS in the LS/W30D model. For LW, the effects  
144 are the same as for LS except for the type of mating which is not included in the model (Table 2).  
145 For ewes born from 1998 to 2017 (68,199 for IF and 78,395 for BMC), EBV\_LS, EBV\_aW30D,  
146 EBV\_mW30D, and EBV\_LW were standardized in genetic standard deviation units. Then, these  
147 EBV\_LS, EBV\_aW30D and EBV\_mW30D were used to compute MAT. Additionally, the average of  
148 these standardized EBVs per year of birth were used to draw the genetic trends for each trait and MAT.  
149 Genetic models were run using a restricted maximum likelihood method implemented in ASREML  
150 software (Gilmour et al., 2014).

151

### 152 **3. Results**

153 Main performances of the two breeds

154 Descriptive statistics for each trait and each breed are presented in Table 3. IF ewes and lambs  
155 performed better than BMC animals. LS (+ 0.13 points) and W30D (+ 0.93 kg) were higher in IF  
156 animals than in BMC. The LW of IF animals was also 2.85 kg heavier than that of BMC animals.

157

158 Genetic parameter estimates for LS

159 All genetic parameter estimates for LS, the trait common to both two-trait models (LS/W30D and  
160 LS/LW models), matched regardless of the model and the breed (Table 4). The additive genetic  
161 variances were between 0.012 and 0.016, the permanent effect variances between 0.004 and 0.010 and  
162 the residual variances between 0.247 and 0.290. The LS repeatability was the same ( $r_{a\_LS} = 0.08$ )  
163 regardless of the breed and the model while LS heritability ranged from 0.04 to 0.06. These parameters  
164 resemble parameters estimated by models that deal only with LS (data not shown).

165

166 Genetic parameter estimates for W30D

167 Although the results were similar, some noticeable differences were observed between the two breeds  
168 for W30D in the LS/W30D model (Table 4). Taking the accuracy of the estimates into account, the  
169 variances of the maternal genetic effect did not differ in the two breeds ( $\sigma^2_{m\_W30D} = 3.87 \pm 0.27$  for IF  
170 and  $\sigma^2_{m\_W30D} = 4.37 \pm 0.26$  for BMC). In contrast, the genetic variance of the direct effect of IF was  
171 twice as low as that of the BMC ( $\sigma^2_{a\_W30D} = 4.64$  for IF vs.  $\sigma^2_{a\_W30D} = 9.79$  for BMC). The maternal  
172 permanent environmental effect was twice as low for BMC as for IF. In both breeds, as the direct and  
173 maternal genetic variance was relatively low, estimated heritability was also relatively low, i.e., less  
174 than 0.10, except for direct heritability for the BMC breed. Finally, the direct and maternal effects were  
175 negatively correlated in both breeds ( $rg_{a\_W30D/m\_W30D} = -0.30$  for IF and  $rg_{a\_W30D/m\_W30D} = -0.45$  for  
176 BMC).

177

178 Genetic parameter estimates for LW

179 The estimated genetic and permanent environmental effect variances of LW were higher in IF than in  
180 BMC (LS/LW model, Table 4). Repeatability and heritability were of the same order of magnitude in  
181 the two breeds and similar to those of LS. Repeatability was 10% and 7% and heritability was 6% and  
182 4% in the IF and BMC breed, respectively.

183

184 Genetic correlations between traits

185 Between LS and the direct effect of W30D, the genetic correlation was medium, positive, and slightly  
186 higher in IF than in BMC:  $rg_{a\_LS/a\_W30D} = 0.31$  for IF and  $rg_{a\_LS/a\_W30D} = 0.22$  for BMC. The genetic  
187 correlation between LS and the maternal effect of W30D was also medium but negative and lower in  
188 BMC than in IF:  $rg_{a\_LS/m\_W30D} = -0.24$  and  $rg_{a\_LS/m\_W30D} = -0.51$ . Between LS and LW, the genetic

189 correlation was positive and high, slightly higher in IF than in BMC:  $r_{g_{a_{LS/a_{LW}}}} = 0.78$  for IF and  
190  $r_{g_{a_{LS/a_{LW}}}} = 0.67$  for BMC (Table 4).

191

192 Genetic progress for MAT, LW and the component traits

193 As reported in figure 1, genetic progress from 1998 to 2017 was lower in BMC than in IF for all the  
194 traits studied. In almost 20 years, the genetic progress in IF was 0.54, 0.23 and 0.59 genetic standard  
195 deviation and 0.47, 0.12 and 0.30 in BMC for direct and maternal effects of W30D and LS,  
196 respectively. The W30D maternal effect was the trait that made the least genetic progress over the  
197 study period with average EBV evolving from - 0.15 to 0.09 genetic standard deviation in IF and from  
198 - 0.07 to 0.05 in BMC. In IF, the genetic trends for the LS and W30D direct effect followed the same  
199 pattern. The MAT curve for the two breeds was close to the LS and W30D direct effect curves. The  
200 genetic progress curve of LW, which is a biological combination of LS, W30D and viability of lambs  
201 at 30 days of age, fell between the LS and the W30D direct effect curves. The Pearson correlation  
202 between EBV\_MAT and EBV\_LW was positive and high: 0.84 for the two breeds.

203

#### 204 **4. Discussion**

205 LS repeatability and heritability were low but in agreement with results in the literature (Maxa et al.,  
206 2007; Lee et al., 2000; Janssens et al., 2004). However, these values were lower than those used in the  
207 French genetic evaluation (Poivey, unpublished data) but similar to more recent estimates (David et al.,  
208 2011). Although LS heritability was low in the two breeds, genetic variances were relatively high and  
209 led to a wide range of genetic values ( $\pm 0.3$  lambs).

210 The variances of the direct genetic and the maternal permanent environmental effect of W30D differed  
211 considerably between the two breeds (Table 4). Although the direct heritability of the W30D was  
212 higher in BMC, it corresponded to the value used in the French official evaluation (Tiphine et al.,

213 2011) as well as in the literature, where heritability estimated direct for pre-weaning weight ranged  
214 from 0.14 to 0.22 across three sheep breeds (Fitzmaurice et al., 2020). On the contrary, the direct  
215 heritability of IF sheep was low, due to relatively low direct genetic variances. Maternal heritabilities in  
216 the two breeds were quite low although still within the extremes reported in the literature (Fitzmaurice  
217 et al., 2020), much lower than those used in French genetic evaluation (Poivey, unpublished data) but  
218 within the range of recent estimates (David et al., 2011). In our study, a negative correlation was found  
219 between the direct additive effect and the maternal genetic effects of W30D. This trend corresponds to  
220 the majority of reports on live weight traits in the literature (Rao and Notter, 2000; Naser et al., 2001;  
221 Boujenane and Kansari, 2002; Safari et al., 2005; Maxa et al., 2007; Gowane et al., 2010; Prince et al.,  
222 2010; Zishiri et al., 2014; Jannoune et al., 2015; Fitzmaurice et al., 2020) with a few exceptions  
223 (Gowane et al., 2014). The most widely supported hypothesis is that of kinship or parental conflict  
224 (Moore and Haig, 1991), which predicts that paternally expressed genes promote extraction of  
225 resources from the mother to enhance fetal and postnatal growth, while maternally expressed genes act  
226 to restrain fetal and postnatal growth to conserve maternal resources (Piedrahita, 2011).

227  
228 The effects used to estimate the genetic parameters of LW was close to the one used for LS (LS/LW  
229 model). Like for LS, the type of oestrus was considered as a fixed effect for LW in view of the high  
230 genetic correlation between LW after natural oestrus and LW after induced oestrus ( $r_g = 0.94$  for IF  
231 and  $r_g = 0.95$  for BMC, data not shown).

232 Part of the total genetic variance is poorly corrected because our model lacks a variation factor, the sire  
233 effect. The proportion of lambs with a known sire was relatively low in the two breeds we studied but  
234 the lambs are purebred, which gives us reason to hope that the sire effect is weak. Bromley et al. (2001)  
235 reported that the variance of effects of mating sires as a fraction of total variance on weaned LW was  
236 low (from 0.00 to 0.03). The large residual variance estimated at 425.39 for IF and at 373.35 in BMC

237 in our study, ranged from 232.9 to 365.7 in Bromley's study (2001) and 713.75 in Duguma's study  
238 (2002). Our estimates of relative variance due to permanent environmental effects were also consistent  
239 with those in the study by Bromley et al. (2001), in which variances of permanent effects were reported  
240 to range from 0.02 to 40.3 in four sheep breeds. In addition, our estimates of the variance of  
241 environmental effects were of the same order of magnitude as the genetic variances in the two breeds.  
242 Estimated repeatability was slightly low to the values reported in the literature. In Bromley et al.  
243 (2001), the average estimated repeatability was similar in the four sheep breeds studied ( $r = 0.13$ ). In  
244 our study, estimated LW heritability was low, close to the heritability of LS. Bromley et al. (2001)  
245 estimated LW heritabilities of the same order of magnitude, ranging from 0.02 to 0.11 for four sheep  
246 breeds. In other studies, the reported estimated heritabilities of LW were somewhat higher ( $h^2 = 0.11$ ,  
247 Rosati et al., 2002) or even much higher ( $h^2 = 0.32$ , Lôbo et al., 2012). This wide range of values can  
248 be explained by the complexity of this trait and the different frameworks used in the studies in the  
249 literature (breed, age at weighing, etc.). Ercanbrack and Knight (1998) attributed litter weight at  
250 weaning to elementary traits like fertility, prolificacy, lamb growth, lamb survival to weaning, and ewe  
251 viability from breeding to weaning, which themselves have low heritability and can, in addition, vary  
252 over time, as is the case for growth.

253 Litter weight is a combination of a reproduction trait at lambing (LS), a production trait during growth  
254 (W30D) and a survival trait during growth (viability at 30 days of age). From a genetic point of view,  
255 the reproduction trait seems to dominate in the combination since the heritability of LW is very close to  
256 that of LS and the genetic correlation between LS and LW is very strong. Moreover, as LS is  
257 moderately correlated with the direct effect of W30D, selection on LW will indirectly and more slowly  
258 improve W30D.

259 Most studies in the literature use litter weight at weaning to characterise ewe productivity. The age at  
260 weaning varies with the breed, cross-breeding, and the production system. In the present study, we used

261 W30D as the basis to estimate maternal traits which are representative of the lambs up to 30 days of  
262 age. Indeed, after 30 days of age, the lamb's diet diversifies and is no longer solely maternal (Prache  
263 and Theriez, 1988). This is why we considered LW at 30 days as a potential alternative selection  
264 criterion to the evaluation of maternal traits. Moreover, to effectively estimate the efficiency of a ewe,  
265 LW can also be linked to the weight of the ewe (Iñiguez and Hilali, 2009) or the metabolic weight of  
266 the ewe can be considered to enable comparison of the production of dams of different size and weight.  
267 Alternatively, the trait could be the total weight of all lambs weaned during the whole production  
268 period of the ewe, weighted by the lifespan of the ewe in order to account for ewe longevity (Duguma  
269 et al., 2002).

270

271 Rao and Notter (2000) reported a positive genetic correlation between LS and the direct effect of  
272 weight at weaning and a negative correlation between LS and the maternal effect of weight at weaning.  
273 Our values are of the same order of magnitude, except for the correlation between LS and the direct  
274 effect of W30D in IF and between LS and the maternal effect of W30D in BMC, which are more  
275 highly correlated. In other studies (Rao and Notter, 2000; Hanford et al., 2005), a positive genetic  
276 correlation was found between LS and the maternal effect of weight at weaning but conclusive  
277 biological interpretations were not included.

278 In our study, estimates of direct genetic correlations between LS and LW were positive and high in  
279 both breeds. These genetic correlations explain the similar genetic trends of LS and LW in figure 1.  
280 However, the genetic correlations reported in the literature are variable:  $0.80 < r_g < 0.99$  in the study of  
281 Bromley et al. (2001),  $r_g = 0.61$  in the study of Duguma et al. (2002) whereas  $r_g = 0.18$  in the study of  
282 Rosati et al. (2002). These differences in genetic correlations are linked to the definition of LW,  
283 particularly age at weighing. In these three studies, lambs were weighed at weaning between 35 and  
284 120 days of age.

285

286 Our results show that selection based on MAT gave a positive correlated response on LW (Figure 1).  
287 Pearson's correlation coefficient estimated between EBV\_MAT and EBV\_LW was high, which also  
288 underlines the direct link between them in IF and BMC. The synthetic maternal index and LW depend  
289 on the same elementary components: LS, W30D and viability of lambs at 30 days of age. For MAT the  
290 breeding values of these components are gathered in a linear combination, while for LW these  
291 components are like elements of a biological "black box" whose breeding value is estimated through a  
292 classical linear model. Since the link between the components of MAT are likely not linear, it would be  
293 useful to run a simulation study to assess which criterion, EBV\_MAT or EBV\_LW, would provide the  
294 higher gain for maternal traits. The genetic trends were quite low for all traits. There are two main  
295 explanations for this result: meat traits were also included in the selection process right from the  
296 beginning, and resistance to scrapie based on the allele of PrP gene was also included starting in early  
297 2000. This new breeding criterion has noticeably reduced the genetic gain especially in BMC, as in this  
298 breed, the original frequency of the resistance allele was low (Palhière et al., 2002).

299

## 300 **5. Conclusion**

301 In France, meat breed ewes are selected for maternal traits based on a synthetic index, MAT,  
302 which  
303 is a linear combination of EBVs for LS, W30D and viability at 30 days of age. As we question the  
304 linearity of the relationship between these three traits in assessing the maternal traits of meat sheep, we  
305 have identified a new potential criterion: LW, which represents an important economic-related trait for  
306 the farmers i.e. the weight of lambs produced per ewe and per lambing. Before any implementation in  
307 breeding programmes, the first step is to estimate the genetic parameters of the new trait. For this  
308 reason, this study aimed to calculate the genetic parameters of LW as a proxy trait to meat production

309 potential of ewes in a French context. Due to its genetic parameters (heritability and animal variance),  
310 LW could be considered as a selection criterion. Its heritability is low, in the order of the estimated  
311 heritabilities for reproductive traits. It would appear that LW, which is biologically dependent on LS,  
312 W30D and lamb viability at 30 days, is strongly dominated by its reproductive trait component.  
313 Moreover, given its genetic correlation, selection based on LW would also increase LS. As LS is  
314 positively correlated with the direct effect of W30D, selection on LW would not degrade the share of  
315 the direct genetic effect of W30D. Finally, MAT and LW are closely related because of the biological  
316 traits on which they depend. This relationship is illustrated by the positive and correlated response on  
317 LW to selection based on MAT last years and by high correlation coefficients between EBV\_LW and  
318 EBV\_MAT.

319

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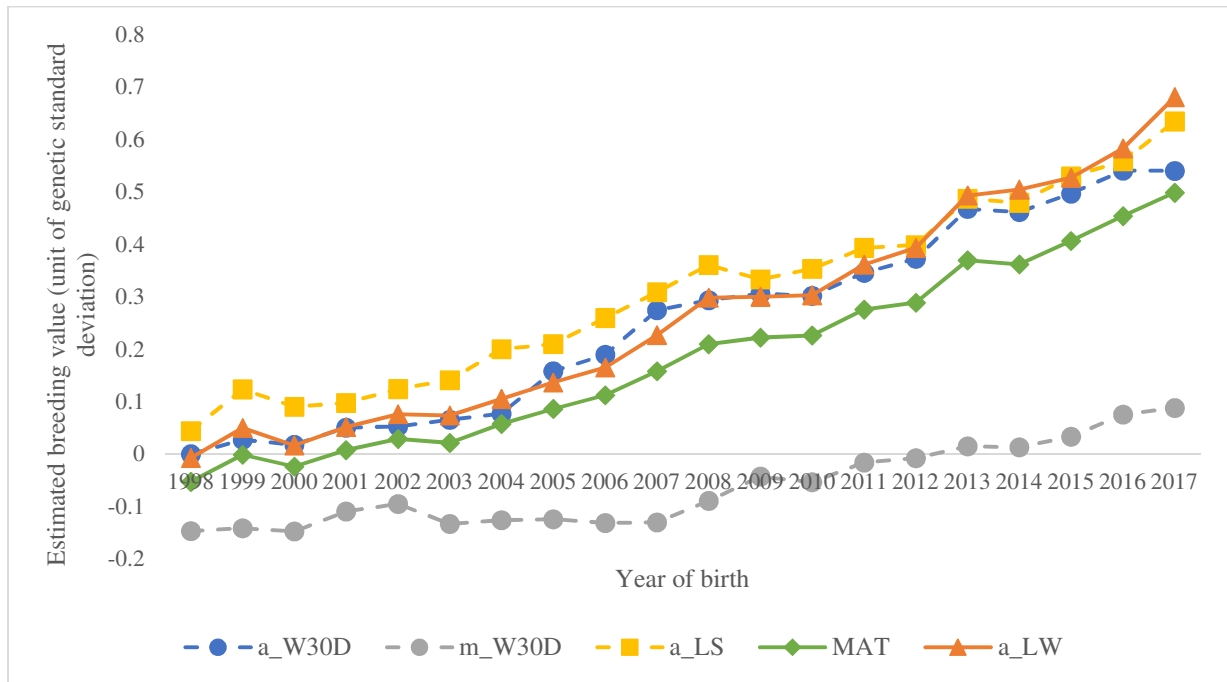
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414

#### 415 **Figures**

416 Figure 1. Genetic trends in litter size at lambing (LS), weight at 30 days of age (W30D), litter weight at  
417 30 days of age (LW), and global index of maternal traits (MAT) for Ile de France (a) and Blanche du  
418 Massif Central (b) ewes born between 2006 and 2018.

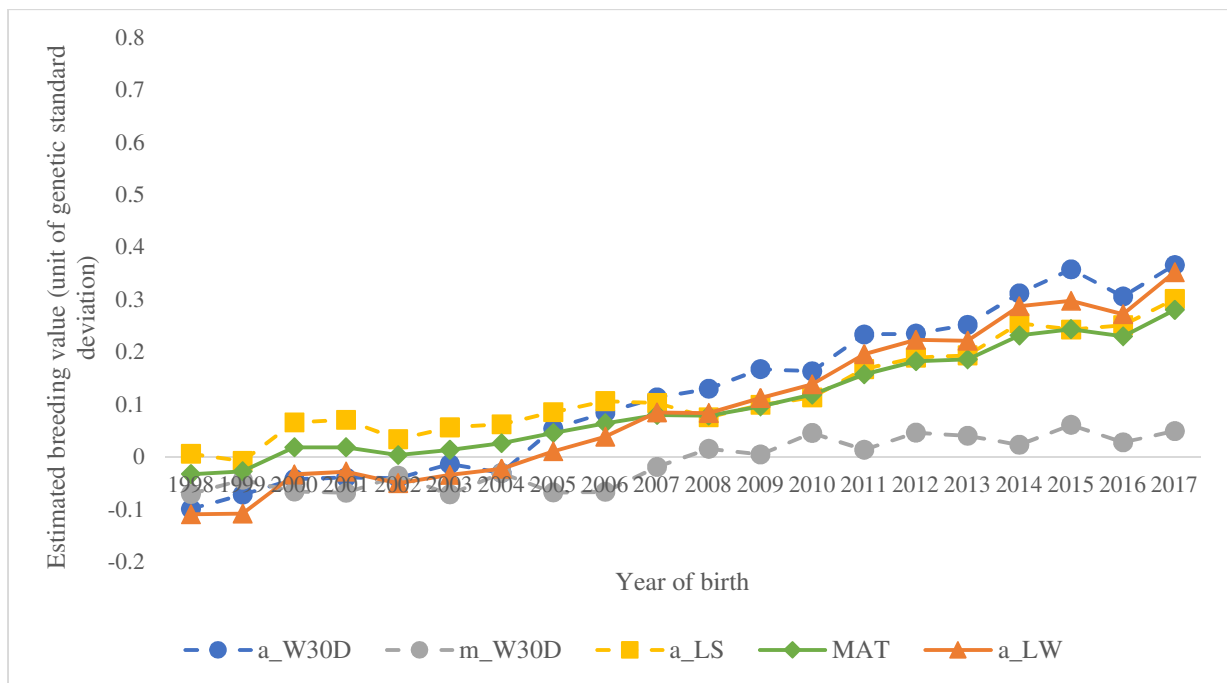
419 (a)



420

421 'a' denotes direct additive genetic effect and 'm' maternal additive genetic effect.

422 (b)



423

424 'a' denotes direct additive genetic effect and 'm' maternal additive genetic effect.

425

426 **Tables**

427 Table 1. Characteristics of the records analysed from 2006 to 2018.

Breed	Ile de France	Blanche du Massif Central
Number of lambs born	302,947	397,362
Number of ewes	73,435	81,733
Number of litters	190,883	271,963
Average number of litters per ewe	2.6	3.3
Number of Herd-Year-Season	2,181	2,087
Percentage lambs with sire information	52.8	33.0
Percentage of mortality	11.4	13.2

428

429 Table 2. Description of fixed effects for each trait in LS/W30D and LS/LW models.

Traits	Fixed effects	Number of levels	Description
	Type of oestrus	2	Natural oestrus
			Induced oestrus
	Type of mating*	2	Natural mating
			Artificial insemination
LS and LW	Physiological status of the ewe	45	Parity
			Age at first lambing
			Lambing interval
			Feeding methods of the ewe lamb (adoption, maternal, artificial and bottle feeding)
			Rearing methods of the ewe lamb (single, twin and more)
			Litter size at the previous lambing
	Month of birth of the ewe	12	January to December
W30D	Physiological status of the	22	Parity

	dam		Age at first lambing
			Lambing interval
			Litter size at the previous lambing
	Overall status of the lamb	36	Age at first weighing
			Rearing methods
			Sex
			Number of males in original litter
	Combination of birth type and rearing methods of the lamb	7	

430 \* This fixed effect is not included for LW

431

432 Table 3. Descriptive statistics for the traits studied for the two breeds, Ile de France (IF) and Blanche  
433 du Massif Central (BMC), from 2006 to 2018.

	Litter size at lambing		Weight at 30 days of age (kg)		Litter weight at 30 days of age (kg)*	
	IF	BMC	IF	BMC	IF	BMC
n	190,883	271,963	268,500	344,944	176,749	246,965
Mean	1.59	1.46	12.44	11.51	19.35	16.50
Minimum	1	1	5.00	5.00	5.00	5.00
Maximum	5	7	20.00	20.00	58.10	58.90
S.D.	0.56	0.54	2.93	2.64	6.50	5.69
C.V. (%)	35.09	36.99	23.55	22.94	33.59	34.48

434 \* Litter weight is presented without correction for sex.

435

436 Table 4. Estimates of variance components, repeatability and heritability (S.E. in brackets) of litter size  
437 at lambing (LS), weight at 30 days of age (W30D) and litter weight at 30 days of age (LW) for Ile de  
438 France (n=73,435) and Blanche du Massif Central (n=81,733) from 2006 to 2018 using multi-trait  
439 models.

Breed	Ile de France		Blanche du Massif Central	
	LS/W30D	LS/LW	LS/W30D	LS/LW
$\sigma^2_{a\_LS}$	0.012 (0.001)	0.015 (0.001)	0.014 (0.001)	0.016 (0.001)
$\sigma^2_{a\_LW}$		28.02 (1.37)		16.55 (0.85)
$\sigma^2_{a\_W30D}$	4.64 (0.31)		9.79 (0.52)	
$\sigma^2_{m\_W30D}$	3.87 (0.27)		4.37 (0.26)	
$\sigma^2_{pe\_LS}$	0.010 (0.001)	0.006 (0.001)	0.007 (0.001)	0.004 (0.001)
$\sigma^2_{pe\_LW}$		20.04 (1.20)		11.95 (0.77)
$\sigma^2_{pe\_W30D}$	4.86 (0.18)		2.93 (0.13)	
$\sigma^2_{e\_LS}$	0.290 (0.001)	0.264 (0.001)	0.282 (0.001)	0.247 (0.001)
$\sigma^2_{e\_LW}$		425.39 (1.64)		373.35 (1.15)
$\sigma^2_{e\_W30D}$	2.96 (0.02)		2.55 (0.04)	
$r_{a\_LS}$	0.08 (0.002)	0.08 (0.002)	0.08 (0.002)	0.08 (0.002)
$r_{a\_LW}$		0.10 (0.003)		0.07 (0.002)
$h^2_{a\_LS}$	0.04 (0.003)	0.05 (0.003)	0.05 (0.002)	0.06 (0.002)
$h^2_{a\_LW}$		0.06 (0.003)		0.04 (0.002)
$h^2_{a\_W30D}$	0.08 (0.005)		0.19 (0.009)	
$h^2_{m\_W30D}$	0.07 (0.005)		0.08 (0.005)	
$rg_{a\_W30D/m\_W30D}$	- 0.30 (0.043)		- 0.45 (0.028)	
$rg_{a\_LS/a\_W30D}$	0.31 (0.053)		0.22 (0.035)	
$rg_{a\_LS/m\_W30D}$	- 0.24 (0.040)		- 0.51 (0.030)	
$rg_{a\_LS/a\_LW}$		0.78 (0.019)		0.67 (0.019)

440 'a' in subscript denotes direct additive genetic effect.

441 'm' in subscript denotes maternal additive genetic effect.

442  $\sigma^2_a$ : direct genetic variance;  $\sigma^2_m$ : maternal genetic variance;  $\sigma^2_{pe}$ : permanent environmental variance

443 where the animal is the ewe for ewe traits and the dam for lamb traits;  $\sigma^2_e$ : residual variance;

444 r: repeatability estimate;  $h^2$ : heritability estimate; rg: genetic correlation.