



HAL
open science

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

Emilie Cobo, Jérôme Raoul, Loys Bodin

► To cite this version:

Emilie Cobo, Jérôme Raoul, Loys Bodin. Genetic parameters of litter weight, an alternative criterion to prolificacy and pre-weaning weight for selection of French meat sheep. *Livestock Science*, 2021, 250, 10.1016/j.livsci.2021.104596 . hal-03272008

HAL Id: hal-03272008

<https://hal.inrae.fr/hal-03272008v1>

Submitted on 2 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

3

4 **Emilie Cobo ^{a,*}, Jérôme Raoul ^{a, b}, and Loys Bodin ^a**

5

6 ^a GenPhySE, INRAE, University of Toulouse, INPT, ENVT, 31326 Castanet-Tolosan, France

7 ^b Institut de l'Elevage, BP 42118 - 31321 Castanet-Tolosan Cedex, France

8

9 *Corresponding author:

10 Emilie Cobo

11 INRAE, UMR1388-GenPhySE

12 24, chemin de Borde Rouge, CS 52627

13 31326 Castanet-Tolosan Cedex – France

14 Tel: +33561285404

15 E-mail: emilie.cobo@inrae.fr

16

17 E-mail co-authors : Jerome.Raoul@idele.fr ; loys.bodin@inrae.fr

18

19

* Corresponding author: emilie.cobo@inrae.fr

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. ± 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 (± 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

320 **Acknowledgements**

321 Sincere thanks to the breeder societies of both breeds for providing data, to Flavie Tortereau and Ingrid
322 David for their methodological support, and to Daphne Goodfellow for her proofreading in English.
323 We would also like to thank the reviewers for their constructive comments.

324

325 **Research Grants**

326 This research did not receive any specific grant from funding agencies in the public, commercial,
327 or not-for-profit sectors.

328

329 **References**

330 Boujenane, I., Kansari, J., 2002. Estimates of (co) variance due to direct and maternal effects for body
331 weights in Timahdite sheep. *Anim. Sci.* 74, 409–414.

332 Bromley, C.M., Van Vleck, L.D., Snowder, G.D., 2001. Genetic correlations for litter weight weaned
333 with growth, prolificacy, and wool traits in Columbia, Polypay, Rambouillet, and Targhee sheep. *J.*
334 *Anim. Sci.* 79, 339–346. doi: 10.2527/2001.792339x.

335 Cheype, A., Guerrier, J., Tortereau, F., François, D., Poivey, J.P., Chile, K., Raoul, J., 2013.
336 Economical weighting of breeding objectives and definition of total merit indexes in BMC sheep breed.
337 64th EAAP annual meeting of the European Association for Animal Production, 26-30 August 2013,
338 Nantes, France. Book of abstracts No. 19, p. 319

339 David, I., Bouvier, F., François, F., Poivey, J.P., Tiphine L., 2011. Heterogeneity of variance
340 components for preweaning growth in Romane sheep due to the number of lambs reared. *Genet. Sel.*
341 *Evol.* 43:32

342 Duguma, G., Schoeman, S.J., Cloete, S.W.P., Jordaan, G.F., 2002. Genetic and environmental
343 parameters for ewe productivity in Merinos. *S. Afr. J. Anim. Sci.* 32, 154–159.

344 Ercanbrack, S.K., Knight, A.D., 1998. Responses to various selection protocols for lamb production in
345 Rambouillet, Targhee, Columbia, and Polypay sheep. *J. Anim. Sci.* 76, 1311–1325. doi:
346 10.2527/1998.7651311x.

347 Fitzmaurice, S., Conington, S.J., Fetherstone, N., Pabiou, T., McDermott, K., Wall, E., Banos, G.,
348 McHugh, N., 2020. Genetic analyses of live weight and carcass composition traits in purebred Texel,
349 Suffolk and Charollais lambs. *Animal.* 14:5, p 899–909. doi: 10.1017/S1751731119002908.

350 Gilmour, A.R., Gogel, B.J., Cullis, B.R., Welham, S.J., Thompson, R., 2014. ASReml User Guide
351 Release 4.1, 337 p.

352 Gowane, G.R., Chopra, A., Prakash, V., Arora, A.L., 2010. Estimates of (co)variance components and
353 genetic parameters for body weights and first greasy fleece weight in Malpura sheep. *Livest. Sci.* 131,
354 94-101. doi: 10.1016/j.livsci.2010.03.006.

355 Gowane, G.R, Chopra, A., Prakash, V., Prince, L.L.L., 2014. The role of maternal effects in sheep
356 breeding: a review. *Indian Journal of Small Ruminants* 20(1), 1-11.

357 Hanford, K.J., Van Vleck, L.D., Snowder G.D., 2005. Estimates of genetic parameters and genetic
358 change for reproduction, weight, and wool characteristics of Rambouillet sheep. *Small Rum. Res.* 57,
359 175–186. doi: 10.1016/j.smallrumres.2004.07.003.

360 Iñiguez, L., Hilali, M., 2009. Evaluation of Awassi genotypes for improved milk production in Syria.
361 *Livest. Sci.* 120, 232–239. doi: 10.1016/j.livsci.2008.07.016

362 Jannoune, A., Boujenane, I., Falaki, M., Derqaoui, L., 2015. Genetic analysis of live weight of Sardi
363 sheep using random regression and multi-trait animal models. *Small Rum. Res.* 130, 1–7. doi:
364 10.1016/j.smallrumres.2015.06.015.

365 Janssens, S., Vandepitte, W., Bodin, L., 2004. Genetic parameters for litter size in sheep: natural versus
366 hormone-induced oestrus. *Genet. Sel. Evol.* 36, 543–562. doi: 10.1051/gse:2004016.

367 Lee, J.W., Waldron, D.F., Van Vleck, L.D., 2000. Parameter estimates for number of lambs born at
368 different ages and for 18-month body weight of Rambouillet sheep. *J. Anim. Sci.* 78, 2086-2090. doi:
369 10.2527/2000.7882086x

370 Lôbo, R.N.B., Junior, G.A.F., Lôbo, A.M.B.O., Faco, O., 2012. Genetic (co)variance components for
371 ratio of lamb weight to ewe metabolic weight as an indicator of ewe efficiency. *Livest. Sci.* 143, 214-
372 219. doi: 10.1016/j.livsci.2011.09.014

373 Maxa, J., Norberg, E., Berg, P., Pedersen, J., 2007. Genetic parameters for growth traits and litter size
374 in Danish Texel, Shropshire, Oxford Down and Suffolk. *Small Rumin. Res.* 68, 312–317.
375 doi:10.1016/j.smallrumres.2005.12.001.

376 Ménissier, F., 1976. Comments on optimization of cattle breeding schemes: beef breeds for suckling
377 herds: a review. *Ann. Génét. Sel. anim.* 8, 71-87.

378 Ménéssier, F., Bouix, J., 1992. L'amélioration génétique en France : le contexte et les acteurs. Les
379 bovins et ovins producteurs de viande. INRA Prod. Anim. Hors série "Eléments de génétique
380 quantitative et applications aux populations animales", 11-23.

381 Moore, T., Haig, D., 1991. Genomic imprinting in mammalian development: a parental tug-of-war.
382 Trends Genet. 7, 45-49. doi: 10.1016/0168-9525(91)90230-N

383 Neser, F.W.C., Erasmus, G.J., van Wyk J.B., 2001. Genetic parameters estimates for pre-weaning
384 weight traits in Dorper sheep. Small Rum. Res. 40, 197-202. doi: 10.1016/S0921-4488(01)00172-9.

385 Palhière, I., François, D., Elsen, J.M., Barillet, F., Amigues, Y., Perret, G., Bouix J., 2002. Allele
386 frequencies of the PrP gene in 29 French sheep breeds. Possible use in selection for resistance to
387 scrapie, in: Proceedings of the 7th World Congress on Genetics Applied to Livestock Production, 2002,
388 CD-Rom n_13-13.

389 Petit, M., Liénard, G., 1988. Performance characteristics and efficiencies of various types of beef cows
390 in French production systems. Compte rendu du 3ème Congrès mondial de reproduction et sélection
391 des ovins et bovins à viande, 19-23 juin 1988, Paris-La Villette. Vol.2, 25-51. INRA, Paris, France.

392 Piedrahita, F. A., 2011. The role of imprinted genes in fetal growth abnormalities. Birth Defects
393 Research (Part A): Clinical and Molecular Teratology 91, 682-692.

394 Prache, S., Theriez, M., 1988. Production d'agneaux à l'herbe. INRA Prod. Anim. 1, 25-33.

395 Prince, L.L.L., Gowane, G.R., Chopra, A., Arora, A.L., 2010. Estimates of (co)variance components
396 and genetic parameters for growth traits of Avikalin sheep. Tropical Animal Health and Production 42,
397 1093-1101. doi: 10.1007/s11250-010-9530-5.

398 Rao, S., Notter D.R., 2000. Genetic analysis of litter size in Targhee, Suffolk, and Polypay sheep. J.
399 Anim. Sci. 78, 2113–2120. doi: 10.2527/2000.7882113x

400 Rosati, A., Mousa, E., Van Vleck, L.D., Young, L.D., 2002. Genetic parameters of reproductive traits
401 in sheep. Small Rum. Res. 43, 65–74. doi: 10.1016/j.smallrumres.2013.11.005

402 Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool,
403 growth, meat and reproduction traits in sheep. *Livest. Prod. Sci.* 92, 271-289. doi:
404 10.1016/j.livprodsci.2004.09.003

405 Tiphine, L., David, I., Raoul, J., Guerrier, J., Praud, J.P., Bodin, L., François, D., Jullien, E., Poivey,
406 J.P., 2011. Estimation of breeding values for meat sheep in France. 62th EAAP annual meeting of the
407 European Association for Animal Production, August 2011, Stavanger, France. Book of abstracts p.
408 344

409 Vanimisetti, H.B., Notter, D.R., Kuehn, L.A., 2007. Genetic (co)variance components for ewe
410 productivity traits in Katahdin sheep. *J. Anim. Sci.* 85, 60–68. doi: 10.2527/jas.2006-248

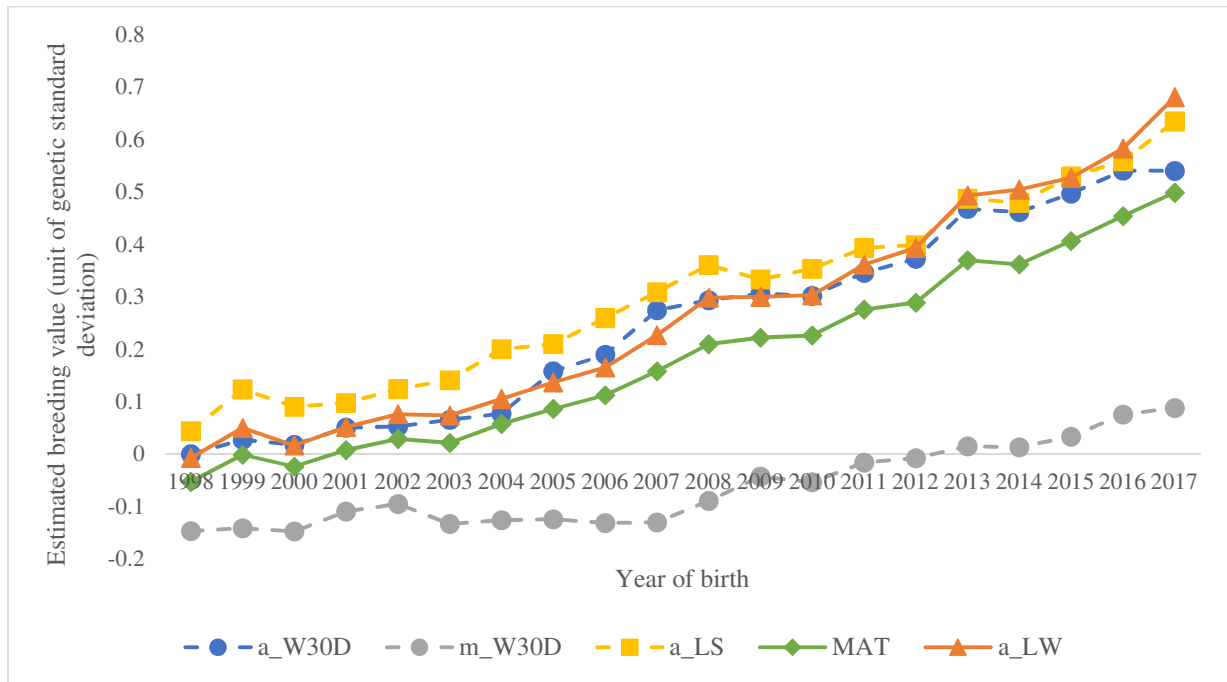
411 Zishiri, O.T., Cloete, S.W.P., Olivier, J.J., Dzama, K., 2014. Genetic parameters for live weight traits in
412 South African terminal sire sheep breeds. *Small Rumin. Res.* 116, 118–125. doi:
413 10.1016/j.smallrumres.2013.11.005

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.

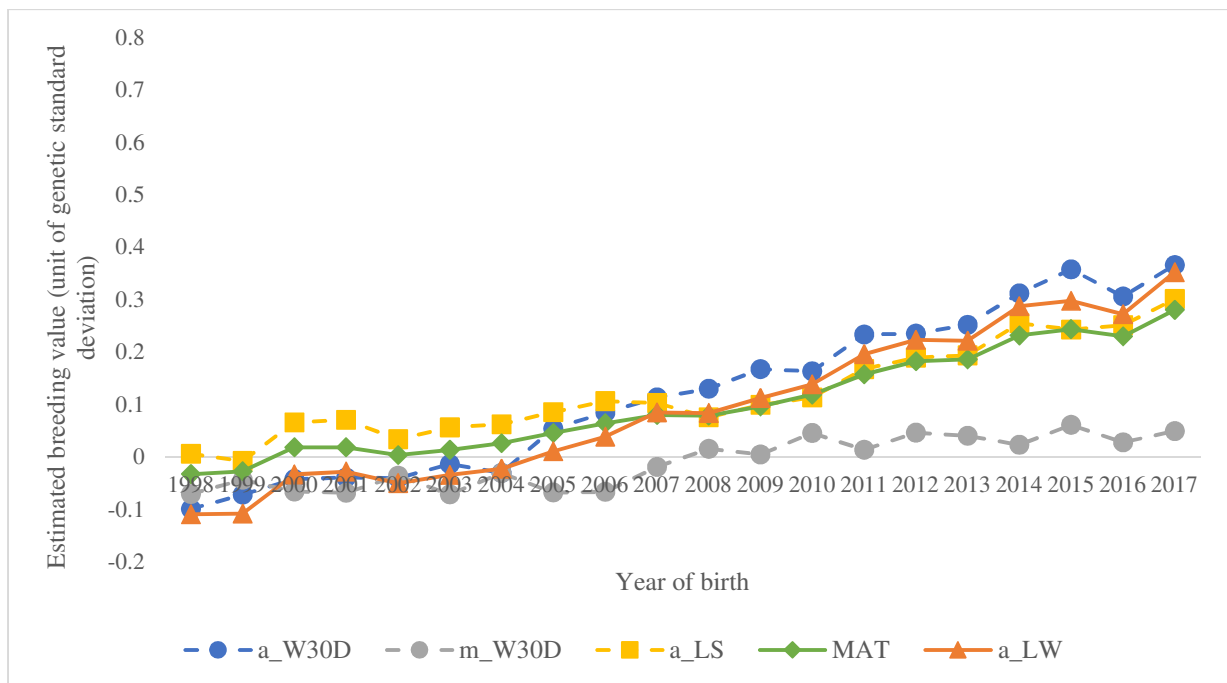
419 (a)



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
LS and LW	Type of oestrus	2	Natural oestrus
			Induced oestrus
	Type of mating*	2	Natural mating
			Artificial insemination
	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)			
Month of birth of the ewe	12	Rearing methods of the ewe lamb (single, twin and more)	
		Litter size at the previous lambing	
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
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	
	Traits model	LS/W30D	LS/LW	LS/W30D
$\sigma^2_{a_LS}$	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 σ^2_a : direct genetic variance; σ^2_m : maternal genetic variance; σ^2_{pe} : permanent environmental variance

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

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