

Relationships between body reserve dynamics and rearing performances in meat ewes¹

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ABSTRACT

The main objective of this work was to study the relationships between body reserve (**BR**) dynamics and rearing performance (**PERF**) traits in ewes from a Romane meat sheep flock managed extensively on “Causse” rangelands in the south of France. Flock records were used to generate datasets covering 14 lambing years (**YR**). The dataset included 1,146 ewes with 2 ages of first lambing (**AGE**), 3 parities (**PAR**) and 4 litter sizes (**LS**). Repeated measurements of the **BW** and **BCS** were used as indicators of BR. The ewe PERF traits recorded were indirect measurements for maternal abilities and included: prolificacy, litter weight and lamb BW at lambing and weaning, ADG at 1, 2 and 3 months after lambing and litter survival from lambing to weaning. The effects of different BW and BCS trajectories (e.g., changes in BW and BCS across the production cycle), previously been characterized in the same animals, on PERF traits were investigated. Such trajectories reflected different profiles at the intraflock level in the dynamics of BR mobilization-accretion cycles. Genetic relationships between BR and PERF traits were assessed. All the fixed variables considered (i.e., YR, AGE, PAR, LS and SEX ratio of the litter) have significant effects on the PERF traits. Similarly, BW trajectories had an effect on the PERF traits across the three PARs studied, particularly during the first cycle (PAR 1). The BCS trajectories only affected prolificacy, lamb BW at birth and litter survival. Most of the PERF traits considered here showed moderate heritabilities (0.17 to 0.23) except for prolificacy, the lamb growth rate during the third month and litter survival which showed very low heritabilities. With exception of litter survival and prolificacy, ewe PERF traits were genetically, strongly and positively correlated to BW whatever the physiological stage. A few weak genetic correlations were found between BCS and PERF traits. As illustrated by BW and BCS changes over time, favorable genetic correlations were found, even if few and moderate, between BR accretion or mobilization and PERF traits, particularly for prolificacy and litter weight at birth. In conclusion, our results show significant relationships between BR dynamics

and PERF traits in ewes, which could be considered in future sheep selection programs aiming to improve robustness.

Key words: body condition score, body weight, genetic parameters, lamb growth, sheep, rangeland

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INTRODUCTION

Breeding for robustness is one of the key identified objectives of the strategy for adapting livestock farming systems to the current and future challenges imposed by climate change and other socioeconomic constraints (Dumont et al., 2014). To address quantitative and qualitative fluctuations in the feed supply, gaining new insights into the physiological and genetic mechanisms affecting the efficiency of the use of body reserves (**BR**) has been reported to be a promising field of research with the aim of optimizing feeding systems while including this trait in future genetic selection programs (Phocas et al., 2016 a, b). This is particularly true for ruminants, for which future farming systems are expected to rely mostly on grasslands and rangelands. It is well known that some typical physiological and environmentally-driven factors have an effect on BR dynamics as reported by the analysis of the relationships between various ewe rearing performances (**PERF**) or mothering abilities and their body condition (Walkom et al., 2014 a, b; Walkom and Brown, 2017).

Walkom and Brown (2017) reported very strong correlations between measurements across the production cycle for BW and BCS along with weak genetic relationships of BW and BCS change traits. These authors suggested that change traits would hold limited value as indirect genetic indicators of growth, carcass and wool traits, and considered that including BCS in the sheep genetics indexes present some merit to improve maternal performance.

Borg et al. (2009) concluded that changes in ewe BW could be a useful indicator of ewe productivity if they reflect changes in, and availability of, body energy reserves during the production year and appear to have an additive genetic component. Their results (Borg et al., 2009) also suggested that ewes with high genetic merit for lamb growth and maternal ability tend to lose more BW in early lactation, presumably as a result of greater milk production, but likewise are capable of compensating for those BW losses through greater subsequent BW gains during breeding and gestation.

We previously provided evidence of the existence of different BR profiles with a genetically-driven component in a Romane meat sheep population in France (Macé et al., 2018, 2019). The first objective of this work was to compare PERF traits between ewes with different BR profiles over several production cycles. We hypothesized that, in Romane ewes, the contrasting BW and BCS profiles that are associated with the different patterns of BR dynamics in a fluctuating pastoral environment are significantly linked to the expression of different rearing abilities (i.e., litter weight and lamb growth rate and survival) both at the intra-cycle level and over several productive cycles. The second objective was to investigate the genetic relationships between BR (i.e. levels and changes over time) and PERF. We hypothesized that PERF traits could be genetically linked to the biological capacity of BR mobilization and accretion.

MATERIAL AND METHODS

Animals and Experimental Farming System

Animal Ethics Committee approval was not required for this study because the data were obtained from existing database sources at INRA (France). The study analyzed data from a Romane meat sheep flock that was reared extensively on 280 ha of rangeland at the INRA Experimental Farm of *La Fage* (Causses du Larzac, 43°54'54.52"N; 3°05'38.11"E; altitude approx. 800 m, Roquefort-Sur-Soulzon, Aveyron, France). The overall characteristics of the experimental farm, the animals and the management have been previously described by Molénat et al. (2005), González-García et al. (2014) and Macé et al. (2018). For the period examined in this study (from 2002 to 2015), the average annual temperature and rainfall were 9.8 °C and 910 mm, respectively.

Before 2010, the first mating age of the females analyzed in this work was 7 mo. of age for ewes with a sufficient weight at mating (i.e., above 40 kg) and 19 mo. of age for ewes with

lower growth rates during the first year (González-García and Hazard, 2016). After 2010, the rearing system was changed to better comply with agro-ecological farming system goals and all first matings were performed at 19 mo. of age. Mating was programmed in autumn to obtain peak lambing at the beginning of spring (usually mid-April) so that the ewes could graze abundant grass during their first month of lactation. The lambs were weaned at approximately 75 ± 4 days. On the *La Fage* farm, an annual culling rate of 30% of the females is applied due to experiments in quantitative genetics. The prolificacy over the years studied averaged 2.2 live lambs per lambing.

Historical Data

All the ewes of this experimental flock are individually monitored for their BW and BCS several times throughout their productive cycles. Their rearing performances and pedigree information are also recorded. The data are recorded in INRA's national database for sheep and goats: GEEDOC (<https://germinal.toulouse.inra.fr/~mcbatut/GEEDOC/>). Regular BW and BCS measurements were performed in order to cover the different physiological stages of the ewes: at mating (-**M**), at early pregnancy (-**Pa**), at mid-pregnancy (-**Pb**), at lambing (-**L**), at early suckling (-**Sa**), at the end of the suckling period (-**Sb**), at weaning (-**W**) and during the post-weaning period (-**Wp**). Over the 14-year period (2002-2015), we recorded data (i.e. BW and BCS at different points of the production cycle) from 2,632 ewes including 1,146 females in first parity (PAR 1; i.e. from first to second mating), 1,072 in second parity (PAR 2) and 414 in third parity (PAR 3). The same two operators systematically recorded the BCS measurements over the 14-year period and underwent regular training sessions for calibration and adjustments while using the scale described by Russel et al. (1969), which was subdivided into 0.1 increments ranging from 1 (emaciated) to 5 (obese). In order to characterize BR changes over time (i.e., accretion or mobilization phases), differences in BW or BCS between pairs of physiological stages were established, calculated and used for

interpretation as described by Macé et al. (2018, 2019). The differences in BW and BCS between different stages were calculated and analyzed (i.e. **BW-Pb:L**, **BCS-Pa:L**, **BW-L:Sa**, **BCS-L:Sa**, **BW-Pb:W**, **BCS-Pa:W**, **BW-M:Pb**, **BCS-M:Pa**, **BW-W:Wp**, **BCS-W:Wp**, **BW-W:M** and **BCS-W:M**).

In order to analyze the ewes' rearing performances, we used the prolificacy of the ewes and defined several traits, based on litter characteristics, as indirect measurements of maternal abilities and performance. These litter traits were the litter weight at birth (**Wlitter-B**) and at weaning (**Wlitter-W**), and the average lamb BW at birth (**Wlamb-B**) and at weaning (**Wlamb-W**). The mean **ADGs** of the lambs in a same litter were used during the first, second and third month after lambing (i.e., **litterADG1m**, **litterADG2m** and **litterADG3m**, respectively). The litter survival at weaning (**litterSurv**) was obtained by considering the number of lambs born and the number of lambs that were alive at weaning. Therefore, for the objectives of this study, all the traits related to the litter characteristics were considered as traits of the ewe's performance.

Descriptive Statistics

To identify sources of variation affecting the PERF traits, the significance of the main effects and first-order interactions were analyzed using the MIXED procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC). The factors tested were the age (**AGE**) at first lambing (1 or 2 years old; classes 1 and 2, respectively), the parity (**PAR**) of the lambing ewe (1, 2 or 3; classes 1, 2 and 3, respectively), the litter size (**LS**) at birth (1, 2, 3 and 4 or more lambs alive; classes 1, 2, 3 and 4, respectively) for **Wlitter-B** and **Wlamb-B**, the **LS** at weaning (1, 2 or 3 lambs weaned; classes 1, 2 and 3, respectively) for **Wlitter-W**, **Wlamb-W** and **litterSurv**, the **LS** during suckling classified by combining the number of lambs born and number of lambs suckled (i.e., class 1, singletons; class 2, ewes lambing twins and suckling one; class 3, ewes lambing and suckling twins; and class 4, ewes lambing and suckling more

than 2 lambs) for litterADG1/2/3m, the **YR** of the measurements (i.e., 14 years corresponding to 14 classes) and the male:female ratio (i.e., the ratio of males born to females born; 9 classes; **SEX**). The first-order interactions of LS×PAR and LS×AGE were tested. An effect was considered significant if $P < 0.05$.

Clustering of individual profiles

Cluster analyses have been performed previously to investigate the variability of individual BW and BCS profiles during each production cycle of the ewe with no assumptions regarding the factors of variation. Several BW and BCS profiles were obtained (see Figure 1 and 2 in Macé et al., 2019). This work has previously been published, and details about the procedures used are available in Macé et al. (2019). In the present study, the relationships between the previously obtained BW and BCS profiles and PERF traits were analyzed and interpreted. The MIXED procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC) was used in order to compare ewe PERF traits for the different BR profiles (clusters).

Genetic Analyses

Animal models were used to estimate heritabilities and repeatabilities for each PERF trait from univariate analyses and to estimate phenotypic and genetic correlations between PERF traits and BR from bivariate analyses. The analyses were performed with the ASREML software (Gilmour et al., 2006) assuming a repeatability model with measurements across productive cycles considered to be the same traits with constant variances. Fixed effects included AGE, PAR, YR, SEX and LS at birth for Wlamb-B and Wlitter-B, LS at weaning for Wlamb-W, Wlitter-W and litterSurv and LS during the suckling period for litterADG1m, litterADG2m and litterADG3m. Random effects included the additive genetic effect and the permanent effect of the ewe. The model was fitted as follows:

$$y = X\beta + Z_a a + W_c c + e \quad [I]$$

where y is the vector of observations for the trait(s) being analyzed, or when considering the litterSurv trait, y is separated into y_1 and y_2 , respectively the vector of observations of the presence/absence of lambs alive at weaning (following a binomial law) and the vector of observations of the number of lambs born, β is the vector of fixed effects, and a and c are the vectors of random ewe additive genetic and permanent environmental effects with incidence matrices X , Z_a , and W_c , respectively, and e is the vector of residual effects.

The following (co)variance structure of random effects was assumed:

$$\text{Var} \begin{bmatrix} a \\ c \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{G}_a \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{P}_c \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where G_a is a (co)variance matrix for direct additive genetic effects, A is the numerator relationship matrix, P_c is a (co)variance matrix for the ewe permanent environmental effects, R is a (co)variance matrix for residual effects, I are identity matrices of appropriate size, and \otimes is the direct matrix product.

From the variance components, 3 parameters were defined as follows: 1) h^2 or proportion of total phenotypic variance attributed to the additive genetic effect, $h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$; 2) proportion of total phenotypic variance attributed to the permanent environmental effect, $c^2 = \sigma_c^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$; and 3) proportion of total phenotypic variance attributed to the residual effect, $e^2 = \sigma_e^2 / (\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$. In addition, the repeatability (r) was defined as the sum of h^2 and c^2 .

RESULTS AND DISCUSSION

The effects of AGE, PAR, LS, SEX and YR and the effects of the interactions PAR×LS and AGE×LS on the rearing performances of the ewes are presented in Table 1. The weight of the litter at lambing, but not at weaning, was affected ($P < 0.001$) by the PAR×LS interaction. Ewes that were older at first lambing, 2-year-old vs. 1-year-old (AGE effect: $P < 0.001$),

lambing heavier litters (9.30 vs. 8.82 kg) with heavier lambs (3.78 vs. 3.55 kg/lamb). The litter weight was affected by PAR and LS at weaning ($P < 0.001$). Ewes at PAR 3 lambing and weaned heavier lambs compared with ewes at PAR 1 (9.85 vs 8.05 kg for Wlitter-B and 42.26 vs 36.39 kg for Wlitter-W), and ewes with higher LS values had heavier litters at birth and at weaning but lighter lambs (Table 1). The litter weight and lamb BW at birth were also affected ($P < 0.001$) by SEX and YR. Ewes lambing more males produced heavier litters with heavier lambs. The lamb BW at lambing was also affected ($P < 0.001$) by AGE, PAR, LS, SEX and YR. The lamb BW increased proportionally with PAR (3.2 vs. 4.0 kg/lamb born at first and third parity, respectively). As the LS increased, the average individual lamb BW decreased (4.7 > 4.0 > 3.1 > 2.8 kg/lamb for LS of 1, 2, 3 or 4 or more lambs at birth, respectively; $P < 0.001$). This parameter was also affected by SEX, the males being heavier than the females. The litter weight at weaning ($P < 0.001$) and lamb BW at weaning ($P < 0.01$) were affected by AGE×LS, with older ewes at lambing producing heavier lambs at weaning. Lamb BW at weaning was not affected by AGE but increased with PAR (i.e. at higher parities, the body weight of lambs at weaning was higher; Table 1).

The AGE, PAR, LS, SEX, YR and the PAR×LS and AGE×LS interactions affected lamb growth rates during suckling (Table 1). The ADG of lambs during their first two months of life was affected by the AGE at which the ewe was mated by first time. Lambs born to ewes lambing at two years of age grew faster than those born to ewes lambing at one year (+10 to +20 g/d). This effect disappeared after 75 days of suckling. Regarding the effects of PAR and LS, the ADG during the three-month suckling period was higher ($P < 0.001$) for lambs born to ewes at PAR 3 than PAR 1 or 2 (+4 to +30 g/d, respectively) and for lambs born as singletons or twins compared with those born in litters of 3 or more lambs (222 vs. 194 g/d, respectively). In contrast to the first two months of suckling, interactions between the main fixed effects did not have an effect on litterADG3m (Table 1). The survival was higher ($P <$

0.001) among the litters of ewes lambing at AGE 1. In contrast, as PAR increased, the litter survival decreased ($0.90 > 0.82 > 0.79$ for PAR 1, 2 and 3, respectively). Surprisingly, the survival rate of singletons was lower than for twins (Table 1). Parity, age at first lambing and sex ratio significantly affected prolificacy.

The relationships between the BW and BCS profiles (i.e., the identified clusters reported by Macé et al., 2019) and the ewes' rearing performances at the intra-parity level are provided in Tables 2 and 3. At PAR 1, all of the parameters were affected by the BW profile with the exception of litterADG3m and litterSurv. The litter weight and lamb BW at birth increased ($P < 0.001$) from clusters BW1 to BW4. As expected, primiparous ewes with lower BW profiles between mating and lambing (clusters BW1 and BW2; Macé et al., 2019) lamb lighter (7.8 ± 0.17 kg; $P < 0.001$) litters with lighter (3.3 ± 0.09 kg; $P < 0.001$) lambs compared with ewes from a higher BW profile (cluster BW3), which averaged 8.5 ± 0.20 and 3.6 ± 0.10 kg for litter weight and lamb BW at birth, respectively. The litter and lamb weights at weaning showed similar differences between the ewe BW clusters suggesting that the effects continued until lambs were weaned. This is consistent with the tendency observed for the ADGs of lambs during the first 2 months after lambing (clusters $BW1 < BW2 < BW3$) with the exception of cluster BW4 (4% of the ewes; see the cyan cluster for PAR 1 in Figure 1; Macé et al., 2019). Cluster BW4, which included ewes with atypical profiles (i.e. maximum BW during suckling), was the cluster with the highest litter weight and lamb BW at birth but the lowest weights at weaning. Prolificacy also increased with higher BW profiles but probably reached a plateau since prolificacy did not increase between BW2 and BW3 clusters. Thus, the performances of primiparous ewes appeared strongly linked to their BW profiles. As hypothesized by Macé et al (2018) for ewes in cluster BW1, the fact that some of the ewes continued to grow themselves during the first reproductive cycle could explain the lower PERF results since such ewes put more energy into their own growth than into production. In

PAR 2 and 3, no differences in litter weight (9.2 ± 0.26 and 9.9 ± 0.37 kg, respectively) or lamb BW at birth (3.8 ± 0.11 and 4.1 ± 0.17 kg, respectively) were detected between the ewes belonging to the different BW profiles. Interestingly, prolificacy was the highest for intermediary BW profiles (i.e. cluster BW6) in PAR2 while there was no significant difference between BW clusters in PAR3. Similarly, no differences were observed for the lamb growth rates during the first month (254 ± 9.2 and 260 ± 10.2 g/d for PAR 2 and 3, respectively; Table 2). During the second month of suckling, however, differences ($P < 0.01$) in the litter ADGs were observed (Table 2) in PAR 2 and 3 between the different BW profiles (BW5 to 8 and BW9 and 10 for PAR 2 and 3, respectively; Macé et al., 2019). At the third month after lambing, differences ($P < 0.05$) between the BW profiles in litterADG3m were only observed for PAR 2. At weaning, the litter weights and lamb BWs were significantly affected by the BW profiles of the ewes in the three PAR values (Table 2). At PAR2, only very slight differences of the PERF traits were observed between the three major clusters. The largest PERF differences at PAR2 and 3 were observed for the clusters containing the smallest proportion of ewes and atypical BW profiles (i.e. clusters BW8 and BW10). Finally, the BW profile of the ewe did not affect litterSurv from lambing to weaning, irrespective of PAR.

Interestingly, ewes in clusters with atypical slopes (BW4, BW8 and BW10; Macé et al., 2019) showed the best PERF trait values for litter weight, lamb BW at birth and litterADG3m, but the worst values for litterADG1m, litterADG2m, and litter weight and lamb BW at weaning. Such low ADG values during the first two months of suckling and the low weight of lambs at weaning could be due to higher energy allocation for maintenance, as suggested by the high increase in BW after lambing in the ewes belonging to these clusters, at the expense of milk production. This lower milk production would decrease the lambs' ADG as has been demonstrated previously with high correlations between milk production and lamb growth

until age 56 d, for ewes of different breeds suckling singletons or twins (Snowder and Glimp, 1991). The high litter ADG_{3m} values for these ewe clusters could be explained by typical compensatory growth effects during the last month of suckling, when the lambs start to graze and become more independent (Torres-Hernández and Hohenboken, 1980). One must keep in mind that these clusters represent only a very small proportion of the whole population.

The only effects of the ewes' BCS profiles were observed on the litter weight and the individual lamb BW for ewes at PAR1 and PAR2 and prolificacy at PAR2 (Table 3). However, at PAR 1, the lower performances observed for the BC3 profile must be interpreted with caution because this cluster represented only 1% of the population studied. At PAR 2, the lower performances of the ewes from the BC6 profile is interesting because this cluster represented 15% of the ewes, 64% of which were from the BC1 profile at PAR1 (Macé et al., 2019). Overall, litter weight and lamb BW were improved when the BCS of the ewe was lower throughout the productive cycle (Table 3; Macé et al., 2019). The same tendency was observed at PAR 3, even though it was not significant. This is likely to be related with mothering ability issues. Ewes with a lower average BCS could be the females that have a better maternal instinct (less "selfish" attitude), always ready to sacrifice their own body condition to answer the needs of their offspring, i.e. BRs mobilized to cover nutrient demands required for fetal growth and development and milk production, during pregnancy and suckling, respectively. Interestingly, prolificacy was the highest in the ewes belonging to the cluster showing the highest BCS profile at cycle 2. In contrast to BW, litterSurv was affected ($P < 0.05$) by the BCS profile but only at PAR 2. The ewes with the lowest BCS profile in PAR 2 (BC5) had higher survival among their litters during suckling (0.88; Table 3), probably due to the same mothering ability arguments discussed above, and the higher levels of energy devoted to lambs mostly during pregnancy rather than during suckling (i.e., higher weight of lambs at birth but similar growth until weaning in the lambs produced by these ewes).

Compared with BW profiles, the relatively weaker overall effects of BCS profiles on PERF traits could be due to the fact that differences between BCS profiles are smaller than between BW profiles.

The estimates of the variance components for the ewe PERF traits are presented in Table 4. Heritabilities were moderate (0.17-0.23) for all traits except litterADG3m, prolificacy and litterSurv (0.08, 0.08 and 0.01, respectively) for which the proportion of phenotypic variance was mainly due to temporary environmental effects (0.91, 0.91 and 0.99, respectively). The repeatability was close to the heritability indicating no additional ewe effects apart from the genetic effect that had an impact on the PERF traits. In agreement with our findings, Everett-Hincks and Cullen (2009) using similar modeling tools reported very low heritabilities for litter survival at different ages until weaning and intermediate heritability values for litter weight traits that ranged from 0.12 to 0.28. Present heritabilities were also similar or slightly higher than those reported by Borg et al. (2009) for lamb weights at birth or weaning considered in their study as lamb traits and not ewe traits.

The genetic and phenotypic correlations between BW or BCS and PERF traits are presented in Table 5 and Supplemental data 1, respectively. The correlations between BW and PERF traits were mostly moderate to high and positive (Table 5), irrespective of the physiological stage, whereas correlations with BCS were mostly low and negative. Ewes with a higher BW were expected to show higher values for the PERF traits whatever the physiological stage. The genetic correlations between BW and PERF traits were highest during suckling and at weaning. These results suggest that BW could be genetically linked to the mothering ability of ewes. Ewes with lower BCS at lambing and until weaning showed higher litter weights and lamb BWs. Such negative correlations could be due to the above discussed effects of mothering abilities (i.e., better mothers are frequently skinny females) and the known related higher energy requirements for these females during the suckling period

(Nielsen et al., 2003; Smith et al., 2017). During BR accretion periods, the negative genetic correlations observed between BCS and PERF traits were unexpected but were however consistent with the higher PERF trait values observed in ewes showing the lowest BCS trajectories. These significant correlations between BCS and PERF traits must be interpreted carefully considering the large standard error. Consistently and complementarily with our findings, Walkom and Brown (2017) reported strong positive genetic correlations between adult ewe BW or BCS and lamb growth. when considering growth as lamb traits.

Relationships between BR and PERF traits were also investigated by considering the changes in BW and BCS over time. Genetic correlations are reported in Table 6 and phenotypic correlations in Supplemental data 2. The genetic correlations between Wlitter-B and BW-M:Pb (0.37) and between Wlitter-B and BW-W:M (0.42) were positive and moderate. These results suggest that the gain in body weight during the BR accretion period (i.e., from weaning to early-pregnancy) is genetically linked to higher litter weight at birth. During pregnancy, we could speculate that such correlations could also be due to an increase in fetus weight. The genetic correlations between BW-Pb:W and Wlitter-B, BW-Pb:L and Wlitter-Bn and between BW-L:Sa and litterADG1m were negative (-0.36 to -0.46; Table 6). These results suggest that increased levels of BW loss during the BR mobilization period spanning from mid-pregnancy to weaning may be related with increased litter weight at birth and higher lamb growth rates during suckling. Such negative, favorable correlations may reflect a higher energy allocation to fetus growth and suckling lambs (Nielsen et al., 2003; Smith et al., 2017) as discussed above. These correlations were in accordance with the positive correlations found between the individual BW measurements (Table 5) and the ewe rearing performances. One cannot exclude that this relationship could also be due to differences in fetus weight since the ewes were weighted just after lambing. However, BW-Pb:L was positively correlated with Wlitter-W, Wlamb-W, litterADG1m and litterADG3m (0.36 to

0.45) which suggests that the decrease in BW during pregnancy (i.e. an increased BW loss during BR mobilization from mid-pregnancy to lambing) is associated with smaller litter weights and lamb BW at weaning and slower lamb growth rates, mainly during the first month (litterADG1). Such correlations contrast with the genetic correlations described between BW-Pb:W or BW-Pb:L and the ewes' rearing performances at lambing. In addition, an unfavorable positive genetic correlation was found between a decrease in BW at late pregnancy and litter survival until weaning, whereas a high favorable negative genetic correlation was found between a decrease in BW at early suckling and litter survival at weaning. It could be expected that the tough environmental conditions of this outdoor pastoral system might have a negative impact on the ewes' rearing performances, with the ewe probably choosing her own survival over that of her offspring thus reducing her reproductive cost (i.e., homeostasis vs. homeorhesis theory, and conservative tactics; Bawman and Currie, 1980; Martin and Festa-Bianchet, 2010). Our results showing genetic relationships between BW changes and PERF traits in ewes are complementary to those reported by Walkom et al. (2014b) who suggested that ewes that are superior at maintaining their BW condition at weaning, would maintain this superiority whatever the number of lambs reared.

Overall, the genetic correlations between BCS changes and ewe rearing performances (Table 6) were negative and moderate for Wlitter-B, during the BR mobilization period from early-pregnancy to weaning (-0.43). This means that the ewes that lose the most body condition over this period produce heavier litters at lambing. This is also consistent with the positive correlation found between BCS-M:Pa and Wlamb-B (0.34). In contrast to Walkom and Brown (2017), who reported moderate negative genetic correlations between weaning weight and BCS loss during suckling, we did not find any significant genetic correlation between BCS losses and milking ability (i.e., lamb growth). Negative correlations (-0.35 and -0.36) were observed, however, between the BCS changes during the BR accretion periods weaning-

post-weaning and weaning-mating and lamb BW at birth. Ewes recovering more body condition during this BR accretion period after mating would produce heavier lambs at lambing but the production of heavier lambs at birth would also be genetically linked with lower BR accretion before mating. This is consistent with the low genetic correlation between BR accretion at early pregnancy and BR accretion after weaning (Macé et al., 2018). Last but not least, consistently with the above results, moderate to high negative favorable genetic correlations between BW-Pb:L or BCS-Pa:L and prolificacy suggest that higher BR mobilization is genetically linked with higher prolificacy. However, these results do not align with the results of Walkom and Brown (2017) and Rose et al. (2014) who found that ewes who lost more weight during late pregnancy showed lower prolificacies.

In conclusion, we demonstrate in this study that the BR profiles of ewes can affect their rearing performances. Overall, the ewes' rearing performances varied between the different BR trajectories (clusters). Ewes with higher BCS profiles and marked body condition decreases (negative slope) and increases (positive slopes) during the BR mobilization and accretion phases, respectively, tended to show better rearing performances. These performances were heritable traits and genetically linked to some periods of BW and BCS changes. Our results argue that taking into consideration BR dynamics in future genetic selection programs aimed at improving ewe robustness may have an impact on ewe performances. Even if our results warrant further research in other sheep populations and environments, increasing ewe robustness through BR management could considerably enhance rearing performances in constraining and challenging environments. Nevertheless, one must keep in mind that animal management and breeding should still be considered in view of present results and those from other teams, for example Walkom et al. (2016) indicating that selection for condition at any time point will lead to more condition at all points and better reproduction.

LITERATURE CITED

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Table 1. Least squares means for ewes' performances (\pm SEM) according to age of the ewe at first lambing (AGE), parity (PAR), litter size (LS), sex ratio of the litter (SEX) and the year of measurement (YR). The significance probabilities for each fixed effects and interactions are provided.

Item	Class	Wlitter-B	Wlamb-B	litterADG1m	litterADG2m	litterADG3m	Wlitter-W	Wlamb-W	litterSurv	prolificacy
<i>n</i>		2628	2628	2632	2632	2631	2632	2632	2632	2632
AGE	1	8.82	3.55	243 (3.72)	223 (3.38)	209 (3.94)	39.27	20.58	0.88	2.15
	2	9.30	3.78	260 (3.54)	234 (3.21)	207 (3.83)	39.96	21.35	0.79	2.26
	Sign.	***	***	***	***	NS	NS	NS	***	***
PAR	1	8.05	3.24	223 (3.80)	208 (3.48)	202 (4.01)	36.39	18.63	0.90	2.13
	2	9.28	3.77	258 (3.39)	233 (3.10)	209 (3.76)	40.19	21.57	0.82	2.23
	3	9.85	4.00	273 (3.96)	245 (3.62)	213 (4.21)	42.26	22.69	0.79	2.26
	Sign.	***	***	***	***	***	***	***	***	***
LS	1	5.10	4.68	302 (5.55)	264 (5.08)	225 (5.92)	23.97	24.11	0.93	
	2	8.78	4.04	264 (4.77)	242 (4.36)	218 (5.16)	41.23	20.85	0.83	
	3	10.17	3.15	224 (3.79)	207 (3.46)	192 (4.05)	53.64	17.93	0.81	
	4	12.20	2.80	215 (3.49)	202 (3.18)	196 (3.63)				
	Sign.	***	***	***	***	***	***	***	***	
SEX	Sign.	***	***	***	***	***	***	***	NS	***
YR	Sign.	***	***	***	***	***	***	***	***	NS
PAR×LS	Sign.	***	NS	***	***	NS	NS	NS	NS	
AGE×LS	Sign.	NS	NS	***	***	NS	***	**	NS	

n = number of records for each trait; Sign. = Significance probability; ** $P < 0.01$; *** $P < 0.001$; NS = non-significant

Wlitter-B = litter weight at birth (kg); Wlamb-B = mean of lamb BW at birth in a litter; litterADG1/2/3m = mean of average daily gain (g/d) for lambs in the same litter during the first, second or third month after lambing; Wlitter-W = litter weight at weaning (kg); Wlamb = mean of lamb weight at weaning (kg) in a litter; litterSurv =litter survival (from lambing to weaning; proportion).

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Table 2. Least squares means and significance probabilities for ewes' performances (\pm SEM) according to BW clusters.

Item	BW cluster ^φ	Wlitter-B	Wlamb-B	litterADG1m	litterADG2m	litterADG3m	Wlitter-W	Wlamb-W	litterSurv	prolificacy
<i>n</i>		1143	1143	1146	1146	1146	1146	1146	1146	1146
PAR 1	BW1	7.72 (0.17)	3.28 (0.09)	241 (10.44)	224 (9.21)	219 (11.85)	40.72 (1.80)	20.00 (1.49)	0.92 (0.01)	2.19 (0.04)
	BW2	7.99 (0.17)	3.40 (0.09)	257 (9.94)	237 (8.77)	225 (11.29)	42.41 (1.80)	21.30 (1.49)	0.89 (0.01)	2.46 (0.04)
	BW3	8.47 (0.20)	3.57 (0.10)	269 (11.14)	252 (9.82)	227 (12.64)	43.98 (1.86)	22.23 (1.54)	0.87 (0.03)	2.53 (0.07)
	BW4	8.51 (0.27)	3.69 (0.14)	251 (14.91)	210 (13.15)	241 (16.92)	38.02 (1.96)	18.10 (1.62)	0.94 (0.03)	2.19 (0.11)
	Sign.	***	***	*	***	NS	***	***	NS	***
<i>n</i>		1068	1068	1068	1068	1067	1068	1068	1068	1068
PAR 2	BW5	9.14 (0.15)	3.80 (0.07)	254 (4.52)	229 (4.04)	212 (5.21)	39.69 (0.49)	21.34 (0.31)	0.83 (0.01)	2.67 (0.10)
	BW6	9.34 (0.18)	3.90 (0.08)	267 (6.92)	240 (6.18)	222 (7.97)	40.80 (0.62)	21.95 (0.40)	0.77 (0.03)	2.92 (0.11)
	BW7	9.06 (0.21)	3.77 (0.09)	255 (6.62)	240 (5.91)	227 (7.62)	40.83 (0.76)	22.02 (0.49)	0.80 (0.03)	2.70 (0.12)
	BW8	9.38 (0.48)	3.80 (0.22)	239 (18.62)	197 (16.64)	233 (21.45)	32.14 (1.91)	17.01 (1.22)	0.81 (0.11)	2.46 (0.23)
	Sign.	NS	NS	NS	**	*	***	***	NS	***
<i>n</i>		406	406	407	407	407	407	407	407	407
PAR 3	BW9	9.73 (0.23)	4.01 (0.10)	270 (5.56)	238 (5.50)	205 (6.81)	41.11 (0.60)	22.06 (0.36)	0.79 (0.02)	2.55 (0.07)
	BW10	10.10 (0.51)	4.10 (0.23)	251 (14.78)	194 (14.62)	209 (18.10)	36.27 (1.98)	18.93 (1.18)	0.73 (0.11)	2.35 (0.22)
	Sign.	NS	NS	NS	**	NS	*	**	NS	NS

n = number of records for each trait; Sign. = Significance probability; **P* < 0.05; ***P* < 0.01; ****P* < 0.001; NS = non-significant; ^φ = As reported by Macé et al. (2019)

PAR = parity; Wlitter-B = litter weight at birth (kg); Wlamb-B = mean of lamb BW at birth in a litter; litterADG1/2/3m = mean of average daily gain (g/d) for lambs in the same litter during the first, second or third month after lambing; Wlitter-W = litter weight at weaning (kg); Wlamb = mean of lamb weight at weaning (kg) in a litter; litterSurv =litter survival (from lambing to weaning; proportion).

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Table 3. Least squares means and significance probabilities for ewe's performances (\pm SEM) according to BCS clusters.

Item	BCS cluster ^φ	Wlitter-B	Wlamb-B	litterADG1m	litterADG2m	litterADG3m	Wlitter-W	Wlamb-W	litterSurv	prolificacy
<i>n</i>		1146	1146	1146	1143	1143	1146	1146	1146	1146
PAR 1	BC1	7.95 (0.16)	3.38 (0.08)	253 (9.53)	232 (8.44)	220 (10.80)	41.60 (1.81)	20.66 (1.50)	0.91 (0.01)	2.30 (0.03)
	BC2	7.96 (0.16)	3.38 (0.09)	252 (9.56)	234 (8.47)	224 (10.84)	41.53 (1.82)	20.58 (1.51)	0.90 (0.01)	2.38 (0.03)
	BC3	6.89 (0.44)	2.74 (0.23)	231 (18.60)	207 (16.46)	215 (21.08)	40.19 (2.36)	19.18 (1.95)	0.91 (0.06)	2.26 (0.20)
	Sign.	*	*	NS	NS	NS	NS	NS	NS	NS
<i>n</i>		1068	1068	1068	1068	1067	1068	1068	1068	1038
PAR 2	BC4	9.16 (0.15)	3.81 (0.07)	254 (4.52)	232 (4.04)	217 (5.23)	39.95 (0.49)	21.48 (0.31)	0.79 (0.02)	2.79 (0.10)
	BC5	9.43 (0.16)	3.93 (0.07)	258 (5.02)	229 (4.50)	216 (5.81)	39.98 (0.54)	21.49 (0.35)	0.88 (0.02)	2.52 (0.11)
	BC6	8.80 (0.18)	3.65 (0.08)	255 (5.63)	229 (5.04)	207 (6.51)	40.22 (0.65)	21.71 (0.42)	0.82 (0.01)	2.71 (0.10)
	Sign.	***	***	NS	NS	NS	NS	NS	*	***
<i>n</i>		406	406	407	407	407	407	407	407	407
PAR 3	BC7	9.79 (0.23)	4.03 (0.10)	269 (5.68)	237 (5.63)	206 (6.94)	40.91 (0.62)	21.93 (0.37)	0.80 (0.02)	2.56 (0.08)
	BC8	9.45 (0.30)	3.91 (0.14)	265 (8.71)	234 (8.63)	189 (10.64)	40.98 (1.12)	22.00 (0.67)	0.78 (0.05)	2.34 (0.12)
	BC9	9.90 (0.32)	4.11 (0.14)	277 (8.39)	240 (8.32)	211 (10.25)	42.16 (1.06)	22.69 (0.63)	0.74 (0.05)	2.63 (0.12)
	Sign.	NS	NS	NS	NS	NS	NS	NS	NS	NS

n = number of records for each trait; Sign. = Significance probability; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = non-significant; ^φ = As reported by Macé et al. (2019)

PAR = parity; Wlitter-B = litter weight at birth (kg); Wlamb-B = mean of lamb BW at birth in a litter; litterADG1/2/3m = mean of average daily gain (g/d) for lambs in the same litter during the first, second or third month after lambing; Wlitter-W = litter weight at weaning (kg); Wlamb = mean of lamb weight at weaning (kg) in a litter; litterSurv = litter survival (from lambing to weaning; proportion).

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Table 4. Estimates (\pm SEM) of variance components for litter traits (ewe performance).

Variable	h^2	c^2	e^2	r	σ_p^2
Wlitter-B	0.17 (0.03)	0.00 (0.03)	0.83 (0.03)	0.17 (0.03)	44.40 (0.13)
Wlamb-B	0.23 (0.04)	0.04 (0.03)	0.73 (0.03)	0.27 (0.03)	6.43 (0.21)
litterADG1m	0.19 (0.04)	0.04 (0.03)	0.78 (0.03)	0.22 (0.03)	2244.10 (69.76)
litterADG2m	0.17 (0.03)	0.00 (0.00)	0.83 (0.03)	0.17 (0.03)	1799.50 (54.12)
litterADG3m	0.08 (0.03)	0.01 (0.03)	0.91 (0.03)	0.09 (0.03)	2793.90 (79.98)
Wlitter-W	0.20 (0.04)	0.00 (0.03)	0.79 (0.03)	0.21 (0.03)	278.09 (8.66)
Wlamb-W	0.22 (0.03)	0.00 (0.00)	0.78 (0.03)	0.22 (0.03)	135.45 (4.21)
litterSurv	0.01 (0.01)	0.01 (0.03)	0.99 (0.01)	0.01 (0.01)	0.02 (0.01)
prolificacy	0.08 (0.03)	0.00 (0.00)	0.91 (0.03)	0.09 (0.03)	0.51 (0.01)

0 h^2 = heritability; c^2 = proportion of total phenotypic variance due to ewe permanent environmental effect; e^2 =
1 proportion of total phenotypic variance due to temporary environmental effects; r = repeatability; σ_p^2 = total
2 phenotypic variance; litterADG1/2/3m=mean of average daily gain for lambs in a same litter during the first,
3 second or third month; Wlitter=litter weight; Wlamb=mean of lamb weight in a litter; -W=at weaning; -B=at
4 birth; litterSurv=litter survival (from lambing to weaning; proportion).

Table 5. Genetic correlations (\pm SE) between BW (A) or BCS (B) at different physiological stages and the ewe rearing performance parameters.

A

Variable	BW-M	BW-Pa	BW-Pb	BW-L	BW-Sa	BW-W	BW-Wp
Wlitter-B	0.32 (0.08)	0.34 (0.08)	0.36 (0.08)	0.30 (0.09)	0.28 (0.09)	0.25 (0.09)	0.34 (0.09)
Wlamb-B	0.33 (0.08)	0.36 (0.08)	0.38 (0.08)	0.30 (0.09)	0.29 (0.09)	0.26 (0.09)	0.35 (0.09)
Wlitter-W	0.55 (0.08)	0.52 (0.08)	0.44 (0.09)	0.57 (0.08)	0.49 (0.09)	0.38 (0.09)	0.45 (0.10)
Wlamb-W	0.57 (0.08)	0.55 (0.08)	0.47 (0.08)	0.62 (0.08)	0.56 (0.08)	0.43 (0.09)	0.49 (0.09)
litterADG1m	0.53 (0.09)	0.54 (0.08)	0.45 (0.09)	0.54 (0.09)	0.46 (0.10)	0.34 (0.10)	0.44 (0.10)
litterADG2m	0.69 (0.07)	0.71 (0.07)	0.64 (0.08)	0.69 (0.08)	0.67 (0.08)	0.56 (0.08)	0.68 (0.08)
litterADG3m	0.57 (0.13)	0.41 (0.14)	0.45 (0.14)	0.63 (0.14)	0.54 (0.14)	0.41 (0.14)	0.39 (0.15)
litterSurv	-0.21 (0.25)	-0.16 (0.24)	-0.24 (0.25)	-0.06 (0.24)	-0.25 (0.26)	-0.26 (0.26)	-0.46 (0.29)
prolificacy	-0.12 (0.13)	-0.09 (0.14)	-0.05 (0.14)	-0.23 (0.14)	-0.19 (0.14)	0.01 (0.15)	-0.06 (0.14)

B

Variable	BCS-M	BCS-Pa	BCS-Pb	BCS-L	BCS-Sa	BCS-Sb	BCS-W	BCS-Wp
Wlitter-B	-0.24 (0.10)	-0.11 (0.10)	-0.12 (0.10)	-0.32 (0.10)	-0.27 (0.10)	-0.19 (0.15)	-0.23 (0.09)	-0.29 (0.10)
Wlamb-B	-0.27 (0.10)	-0.10 (0.10)	-0.11 (0.10)	-0.31 (0.10)	-0.24 (0.10)	-0.19 (0.15)	-0.19 (0.10)	-0.28 (0.11)
Wlitter-W	-0.20 (0.12)	-0.08 (0.11)	-0.11 (0.11)	-0.02 (0.12)	-0.06 (0.12)	-0.28 (0.15)	-0.16 (0.11)	-0.15 (0.13)
Wlamb-W	-0.22 (0.12)	-0.09 (0.11)	-0.04 (0.11)	-0.01 (0.12)	-0.03 (0.12)	-0.30 (0.15)	-0.15 (0.11)	-0.14 (0.12)
litterADG1m	-0.30 (0.12)	-0.21 (0.12)	-0.22 (0.12)	-0.11 (0.13)	-0.09 (0.13)	-0.34 (0.15)	-0.26 (0.11)	-0.21 (0.13)
litterADG2m	-0.15 (0.13)	-0.06 (0.12)	-0.00 (0.12)	0.05 (0.12)	-0.06 (0.12)	-0.25 (0.16)	-0.13 (0.11)	-0.05 (0.13)
litterADG3m	-0.28 (0.16)	-0.22 (0.15)	-0.34 (0.14)	-0.27 (0.16)	-0.34 (0.15)	-0.30 (0.20)	-0.35 (0.14)	-0.32 (0.16)
litterSurv	-0.14 (0.24)	-0.21 (0.23)	0.01 (0.23)	-0.04 (0.25)	-0.15 (0.25)	-0.57 (0.26)	-0.18 (0.25)	-0.37 (0.25)
prolificacy	0.04 (0.16)	0.04 (0.15)	-0.07 (0.15)	-0.29 (0.15)	-0.38 (0.14)	0.11 (0.20)	-0.01 (0.16)	-0.26 (0.14)

BW = body weight; BCS = body condition score; M = mating; Pa = early pregnancy; Pb = mid pregnancy; L = lambing; Sa = early suckling; Sb = mid suckling; W = weaning; Wp = post-weaning; litterADG1/2/3m = mean of average daily gain for lambs in a same litter during the first, second or third month; Wlitter = litter weight; Wlamb = mean of lamb weight in a litter; -W = at weaning; -B = at birth; correlations in bold are significant.

Table 6. Genetic correlations (\pm SE) of BW variations (A) or BCS variations (B) between different physiological stages and the ewe rearing performance parameters.

A						
Variable	BW-M:Pb	BW-Pb:W	BW-Pb:L	BW-L:Sa	BW-W:Wp	BW-W:M
Wlitter-B	0.37 (0.14)	-0.36 (0.14)	-0.36 (0.15)	-0.04 (0.19)	0.17 (0.16)	0.42 (0.15)
Wlamb-B	0.20 (0.14)	-0.28 (0.14)	-0.01 (0.15)	-0.10 (0.18)	0.24 (0.16)	0.28 (0.15)
Wlitter-W	-0.11 (0.15)	-0.21 (0.14)	0.42 (0.15)	-0.31 (0.18)	0.27 (0.15)	0.24 (0.15)
Wlamb-W	-0.09 (0.15)	-0.18 (0.14)	0.43 (0.14)	-0.18 (0.19)	0.23 (0.15)	0.31 (0.14)
litterADG1m	-0.22 (0.16)	-0.29 (0.15)	0.45 (0.16)	-0.46 (0.19)	0.35 (0.16)	0.37 (0.15)
litterADG2m	0.09 (0.15)	-0.29 (0.14)	0.01 (0.15)	0.05 (0.19)	0.25 (0.16)	0.25 (0.16)
litterADG3m	-0.08 (0.20)	-0.13 (0.19)	0.36 (0.19)	-0.32 (0.23)	-0.10 (0.21)	-0.25 (0.20)
litterSurv	-0.24 (0.31)	-0.04 (0.30)	0.61 (0.26)	-0.72 (0.33)	0.12 (0.31)	-0.02 (0.30)
prolificacy	0.28 (0.18)	-0.22 (0.18)	-0.62 (0.14)	0.29 (0.23)	-0.08 (0.21)	0.24 (0.19)
B						
Variable	BCS-M:Pa	BCS-Pa:W	BCS-Pa:L	BCS-L:Sa	BCS-W:Wp	BCS-W:M
Wlitter-B	0.34 (0.17)	-0.43 (0.13)	-0.42 (0.15)	-0.07 (0.20)	0.16 (0.19)	0.08 (0.19)
Wlamb-B	0.34 (0.16)	0.03 (0.14)	-0.14 (0.15)	0.05 (0.19)	-0.35 (0.16)	-0.36 (0.17)
Wlitter-W	0.25 (0.16)	-0.20 (0.14)	0.07 (0.15)	-0.10 (0.20)	0.11 (0.19)	0.17 (0.17)
Wlamb-W	0.25 (0.16)	-0.21 (0.14)	0.09 (0.14)	-0.11 (0.19)	0.14 (0.18)	0.25 (0.16)
litterADG1m	0.16 (0.17)	-0.18 (0.15)	0.14 (0.15)	-0.08 (0.20)	0.20 (0.19)	0.33 (0.17)
litterADG2m	0.27 (0.17)	-0.20 (0.14)	0.07 (0.15)	-0.24 (0.19)	0.16 (0.19)	0.27 (0.17)
litterADG3m	0.17 (0.22)	-0.23 (0.19)	-0.09 (0.20)	-0.05 (0.25)	0.03 (0.24)	0.04 (0.23)
litterSurv	-0.14 (0.31)	-0.06 (0.29)	0.31 (0.26)	-0.24 (0.32)	-0.25 (0.32)	-0.62 (0.22)
prolificacy	-0.03 (0.02)	-0.27 (0.17)	-0.36 (0.17)	0.02 (0.24)	0.18 (0.22)	0.28 (0.21)

BW = body weight; BCS = body condition score; M = mating; Pa = early pregnancy; Pb = mid pregnancy; L = lambing; Sa = early suckling; Sb = mid suckling; W = weaning; Wp = post-weaning; litterADG1/2/3m = mean of average daily gain for lambs in a same litter during the first, second or third month; Wlitter = litter weight; Wlamb = mean of lamb weight in a litter; -W = at weaning; -B = at birth; correlations in bold are significant.