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PhenoBR: a model to phenotype body condition dynamics in meat sheep

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Abstract

In situations of negative energy balance (**NEB**) due to feed scarcity or high physiological demands, body energy reserves (**BR**), mainly stored in adipose tissues, become the main sources of energy for ruminants. The capacity to mobilize and restore such BRs in response to different challenges is of major concern in the current context of breeding for resilience. Body condition score (**BCS**) is a common, practical indicator of BR variations throughout successive productive cycles, and quantitative tools for characterizing such dynamics at the individual level are still lacking. The main objective of this work was to characterize body condition dynamics in terms of BR mobilization and accretion capacities of meat sheep during their productive lifespan through a modelling approach, using BCS measurements. The animal model used in this work was the reproductive meat ewe (*n* = 1478) reared in extensive rangeland. Regular measurements of BCS for each productive cycle were used as the indicator of BR variations. A hybrid mathematical model and a web interface, called PhenoBR, were developed to characterize ewes' BCS variations through four synthetic and biologically meaningful parameters for each productive cycle i: BR accretion rate (k_b^i), BR mobilization rate (k_p^i), plus the time of onset and the duration of the BR mobilization, t_b^i and ΔT^i, respectively. The model PhenoBR converged for all the ewes included in the analysis. Estimation of the parameters indicated the inter-individual variability for BR accretion and mobilization rates, and the length of the mobilization period. The present study is a proof of concept that the combination of data-driven and concept-driven models is required for the estimation of biological meaningful parameters that describe body reserves dynamics through consecutive productive cycles. Individual characterization of animals by these parameters makes it possible to rank them for their efficiency in the use of body reserves when facing NEB challenges. Such parameters could contribute to better management and decision-making by farmers and advisors, e.g. by adapting feeding systems to the individual characteristics of BR dynamics, or by geneticists as criteria to develop future animal breeding programs including BR dynamics for more robust and resilient animals.

Keywords: mathematical model, body reserves' dynamic, ruminant, Negative energy balance, resilience

Implications

In situations of negative energy balances, the capacity of meat sheep to mobilize and restore their body reserves is of major importance in the current context of breeding for resilience. In this respect, PhenoBR suggests a modelling approach to describe body condition score dynamic with four quantitative parameters for each parity at individual level. Such parameters could contribute to better adapting feeding systems to the individual characteristics of body reserves dynamics, and by geneticists as criteria to develop future animal breeding programs including body reserves dynamics for more resilient animals.

Introduction

Body energy reserves (**BR**) are the main source of energy in ruminants facing negative energy balance (**NEB**) challenges such as highly demanding reproductive cycles or feed scarcity periods (Bauman and Bruce Currie, 1980; Chilliard et al., 1998). The capacity of ruminants to mobilize and restore such BRs in response to challenges is of major concern in the current context of breeding for robustness and resilience, and for the ultimate sustainability goals of farming systems. Resilience is a defined as the capacity to recover after short-term perturbations in the environment or changes in animal's physiological state, while robustness is the capability of the animal to maintain its performance (considering several performance indicators and different levels) and deal with unfavourable environments over long terms (Colditz and Hine, 2016; Friggens et al., 2017). However, it is worth mentioning that these two terms are often interlinked and robustness at a given level is the result of resilience at underlying levels. In this respect, priorities chosen by complex mechanisms related to nutrient allocation and trade-offs become critical at the individual level. BR administration and operational feeding strategies are among the main resources set by the animal and the farmer, respectively, to cope with such challenges.

In meat sheep, a broad intra-flock variability in the dynamic of BR was shown during their lifespan including several reproductive cycles. The genetic determinism related to the BR changes has been demonstrated by considering successive physiological stages independently (Macé et al., 2018, 2019). The BR dynamics could be considered in selection strategies designed to improve the ewes' adaptive capacities while maintaining production and welfare. It is therefore of major interest to phenotype ewes for their capacity of resilience in situations of NEB.

Despite the importance of BR dynamics for animal robustness, its use in animal husbandry and breeding is still at its very early stages (Kitano, 2004; Friggens et al., 2017). There are two main reasons for this. Firstly, there is a lack of dynamic data describing animal response in a short-, medium- and long-term perspective when facing different, successive challenges of different magnitude and amplitude. However, progress in technology in the last decades has made it possible to measure several indicators of animal performance with relatively high frequency (i.e. dynamic records). Through the development of new technologies, the monitoring of dynamic measures and indicators such as body weight, milk yield and feed intake are now possible with higher frequency and at lower cost. Secondly, the absence of synthetic criteria for characterizing and quantifying BR dynamics is still a limiting factor for the use of such a complex phenotype. Body condition score (**BCS**) is a practical and conventionally used variable for monitoring BR dynamics. Compared to other variables such as BW, BCS is a proven reliable indicator of the status of an animal's body fat reserves (Russel et al., 1969; Mendizabal et al., 2011). Although some automatic advances are available, BCS continues to be a subjective but effective variable, measured in general through direct observations carried out by a trained observer (Schröder and Staufenbiel, 2006; Pearce et al., 2009). In outdoor farming systems (e.g. grazing, rangelands, etc.) there are still limitations to overcome regarding, for example, the availability of ultrasound tools for implementing automatic measurement of BCS at the individual level in open environments.

Subjective estimates of body condition have been widely used for a relatively long time to assess fat in the live animal. Murray (1919) defined body condition as 'the ratio of the amount of fat to the amount of non-fatty matter in the body of the living animal. In the method used in the experimental farm from which we collected the historical database analysed in this study, the prominence of the spinous processes of the anterior lumbar vertebrae is assessed by palpation. The BCS was assessed by a trained operator according to an adaptation of the original grid described by Russel et al. (1969) which was further divided into a 1/10 scale, i.e., from 0 to 5 with 0.1 increments. In the specific case of females, this information indicates a strong link with her reproductive performance, and the potential percentage of open females, lambing interval, and lamb vigour at birth being among other parameters, all closely related to the body condition of the ewe both at lambing and during the breeding season and lactation periods (Debus et al., 2022). Finally, it is important to be aware that the particular characteristics of the breed can have a strong influence on where and how body fat is deposited.

Macé et al. (2018) concluded on the usefulness of BCS and BW data to study the capacity of BR mobilization and accretion in meat ewes. Based on mean trajectories of BCS and BW, they defined periods of mobilization and accretion throughout ewes' lifespans and studied variations of BCS and BW in different physiological stages during these periods. Some dynamic and mechanistic models were developed to predict fat fluxes in cattle during transition periods, using BCS and DMI (Tedeschi et al., 2013) and to describe BR variations in dairy goats during their lifespan using daily measurement of BW (Puillet and Martin, 2017). However, to our knowledge, there is no tool still available for individual treatment of BCS data in sheep to automatically detect periods of BR mobilization and accretion and to quantify the related variability of individual responses to NEB challenges in a given common flock or population.

The objective of the present work was to produce a quantitative, integrated tool to quantify resilience capacity of meat ewes to the short-term physiological challenge during the reproductive cycle. To this end, BR dynamics of meat ewes reared outdoors were characterized with four synthetic variables at each parity. To do so, a dynamic model, called PhenoBR, was developed, based on a system of ordinary differential equations, as a support tool to describe BCS variations in meat ewes over several productive cycles. This model is implemented in a web interface (http://adaptive-capacity.herokuapp.com/) that lets users (even those unfamiliar with modelling) test different hypotheses and results of the model. This tool could be used for investigating physiological and genetic components of BR dynamics during this challenging period and developing future animal breeding programs for more robust and resilient animals.

Material and Methods

The animal used in this work was the reproductive meat ewe, during its whole lifespan. However, the model can be considered as generic and adaptable to ruminant species and productive purposes after some necessary adjustments and calibrations. The parameters of this model represent the ewe's characteristics in terms of its capacities to mobilize and restore BR at each production cycle. The model has two types of parameters. The first category comprises time-related parameters (i.e. time related to the beginning of BR mobilization and the interval, or duration of the BR mobilization period for each productive cycle). The second category of parameters is related to the intensity of the BR mobilization period and the capacity to recover an expected BR status. The model is hybrid in that it combines a data analysis procedure and a more concept-driven model.

Animals and experimental data

The datasets used in the present study have been previously described in detail (Macé et al., 2018, 2019). Briefly, the experimental animals belonged to the Romane meat sheep breed. The monitored ewes (*n* = 1478) were reared under extensive conditions on the rangelands of the INRAE La Fage experimental farm (Causse du Larzac 43°54’54.52”N; 3°05’38.11”E, Roquefort du Soulzon, France). Ewes performed one productive cycle per year. The biological productive cycle length was thus 365 days. Data were collected for the period 2002 to 2015.

In this study, the BCS was used as the main indicator to illustrate the BR dynamics (i.e. the capacity of ewes to mobilize and restore BRs). Ewes were measured for BCS, with eight measurements collected regularly during each female's productive cycle according to a physiological stage schedule. Ewes were measured during one to three entire productive cycles (1278 ewes for cycle 1, 1204 ewes up to cycle 2 and 521 ewes up to cycle 3). All ewes included in the present study were pregnant and suckled at least one lamb until weaning (~80 days after lambing). To assess BCS, the original grid described by Russel and coworkers (Russel et al., 1969) was used and subdivided into a 1/10 scale, i.e. from 0 to 5 with 0.1 increments. As a subjective method, considerable variations in score may be expected both between and within observers. To reduce this variation, only two operators performed the BCS measurements throughout the entire period of the study. Although, no quality control was performed, observers followed regular training sessions for adjustments and calibration during that period, which guarantee the reliability of BCS measures. All measurements were recorded in the Geedoc database (https://germinal.toulouse.inra.fr/~mcbatut/GEEDOC/).

Modelling procedure: General model

To characterize the ewes' response to the increasing energy requirements at each productive cycle in terms of BCS variations, a system of ordinary differential equations was developed. For present purposes, the large increase in energy requirements during a productive cycle due to pregnancy and suckling is termed perturbation. The objective of model development is to describe the ewe's response to that perturbation using BCS variation as the indicator of ewe's response. Two interrelated state variables were used to describe the ewe's response at productive cycle i: p_i for the decrease in BCS during the mobilization period and BCS_i for the variations in BCS during the same productive cycle including its decrease by p_i and its recovery (Fig 1). The driving force of this model is the intrinsic capacity of the ewes to maintain or to restore their BRs to reach the expected BCS, considered as the value of BCS in the absence of perturbations, noted BCS_m. The concept of the expected trajectory of performance is already described in the literature (Nguyen-Ba et al., 2020). In the database used, the ewe population attained at most three productive cycles, and the total BCS variations was calculated as the sum of BCS_i variations, for $i \in \{1,2,3\}$.

The general model for one productive cycle could then be written as Equation 1.

$$dBCS_i(t)/dt = \text{Accretion} - \text{mobilization} \qquad \text{Equation 1}$$

For productive cycle i, periods of BR mobilization and accretion are both assumed to start from the point when BCS_i starts to decrease (t_b^i), considered as the starting point of the perturbation being studied. When the animal is no longer able to meet the energy demands induced by pregnancy and lactation using only the energy available from ingested feeds, it will mobilize the energy stored in its adipose tissues (i.e. its energetic BRs). However, during and after this period, the animal uses internal mechanisms to limit or to compensate for the quantity of BRs used during this period. This is illustrated by the effort of the animal to reach BCS_m. To clearly separate the effects of each productive cycle, the BR recovery capacity associated with productive cycle i starts at t_b^i and lasts until the beginning of the next productive cycle (t_b^{i+1}). The BR mobilization period is assumed to be over at t_e^i, which is the end of the BCS decrease period (i.e. end of perturbation$i$). t_e^i is associated with the point where the capacity of BR accretion surpasses the ewe's energy requirement. Equations 2.a and 2.b describe the variations in BCS_i and the simultaneity and continuity of BR mobilization and accretion processes for productive cycle i.

$$dp_i/dt = k_p^i(p_m - p_i) \text{ for } t \in [t_b^i, t_e^i]), \qquad \text{Equation 2.a}$$

$$dBCS_i/dt = k_b^i(BCS_m - BCS_i) - k_p^i(p_m - p_i) \text{ for } t \in [t_b^i, t_b^{i+1}]), \qquad \text{Equation 2.b}$$

Where $[a,b] = \{x|\ a \leq x \leq b\}$. The constants p_m and BCS_m stand for the maximal loss of BCS due to a perturbation and the expected value of BCS_i, respectively. k_b^i and k_p^i are the rates for BR accretion and mobilization during the productive cycle i, respectively. Variations in total BCS during the ewe's lifespan are the sum of variations of BCS_i at each productive cycle as stated in Equation 3.

$$\mathrm{d}BCS/\mathrm{dt} = \sum_{i=1}^{3}\left[k_b^i(BCS_m - BCS_i).\left(t \in [t_b^i, t_b^{i+1}]\right) - k_p^i(p_m - p_i).\left(t \in [t_b^i, t_e^i]\right)\right]$$

$$BCS_i^{init} = BCS(day = t_b^i), BCS^{init} = BCS(day = t_b^1),$$

$$p_i^{init} = 0\ ; P_m = 2 \text{ unit of BCS },$$

$$i = 1,2,3 \qquad \text{Equation 3}$$

where BCS_i^{init} is the initial value of BCS_i, and BCS^{init} is the initial value of the total BCS. P_m is defined as the maximum loss of BCS, and its value should respect the minimum value of BCS for the ewe to survive (considered as 2 in this study). Using this model, the response of the animal at each productive cycle is characterized by the set of parameters $\{k_b^i, k_p^i, t_b^i, \Delta T^i\}$, where $\Delta Ti = t_e^i - t_b^i$, and stands for the duration of the mobilization period. Parameters k_b^i and k_p^i are estimated using the minimization function in Equation 4

$$f_{obj} = \min\left(\sqrt{\Sigma_{j=1}^{N}[obs_j - BCS(t_j)]^2}\right), \qquad \text{Equation 4}$$

where j stands for the number of observation points obs_j of BCS during the ewe's lifespan, and $BCS(t_j)$ is the estimation of BCS at age t_j by the model (Equation 3). N is the number of observations for a given animal (at most $N = 24$). Other parameters of the model are time-related t_b^i and ΔT^i, which are determined using a data analysis procedure for automatic detection of the perturbation within each productive cycle. The dataset involved ewes with 1, 2 or 3 parities, and the data analysis procedure allowed automatic determination of the number of parities to be considered for each ewe, and the beginning and the duration of the associated perturbation.

Global sensitivity analysis (Saltelli et al., 1999; Taghipoor et al., 2016) was used to calculate the fraction of the BCS variance explained by k_b and k_p. The sensitivity indices were calculated for a hypothetic example of BCS variations for only one parity, for the BCS output at three time points before the end of perturbation t_e, and three time points after t_e (details are presented in supplementary code S1 and Table S1).

Modelling procedure: Automatic detection of perturbation period

The beginning and end of each productive cycle ware taken to be from one mating to the subsequent one. When all data were missing in a given period, it was taken as a missing productive cycle. In this section, a data analysis procedure based on functional data analysis (**FDA**) was developed to automate detection of perturbations within each productive cycle. In this procedure, the beginning of a perturbation (t_b^i) is where the observed BCS started to deviate from the initial value of BCS_i (BCS_i^{init}). The end of the perturbation (t_e^i) is where it started to recover (see Fig 2 for details).

The expected value of BCS (BCS_m) is determined depending on the observed maximum value of BCS (BCS_{max}) for each individual. For ewes with $BCS_{max} < 3.4$ then the of value of $BCS_m = 3.5$, otherwise for ewes with $BCS_{max} < 4$, the value of $BCS_m = 4$. The value of 3.4 was chosen because it was the common observed maximum BCS value for most of the ewes in the dataset. The maximum value of BCS for all other ewes, remains smaller than 4. Also, in the construction of PhenoBR, the value of threshold BCS_m will be approached but never reached. It should therefore be larger than BCS_{max}, to let ewes reach their BCS_{max}. A B-Spline regression with smoothing parameters $\lambda = 10^3$ was fitted to the BCS data of each animal. This regression is in particular useful in cases where the general shape of the function under study is unknown, which is the case in the presence of perturbations. Equation 5 describes the objective function to fit the B-spline function to observed data, for the estimation of the function $BCS(t)$.

$$J_{obj} = \min\left(\Sigma_{j=1}^{N}[obs_j - BCS(t_j)]^2 + 10^3\int_0^{t_{max}}[\,\partial^2 BCS(t)]^2 dt\right) \qquad \text{Equation 5}$$

Where obs_j stands for the jth observation of BCS, $BCS(t_j)$ is the estimation of BCS by the B-spline function and t_{max} is the last day of the BCS record for each individual.

Zeros of the derivative of the estimated function $BCS(t)$ are maximums and minimums of $BCS(t)$. This regression is drawn from methods on analysis of functional data (Ramsay and Silverman, 2002; Codrea et al., 2011; Nguyen-Ba et al., 2020), in which the flexibility of the fitted function is ensured by the use of the piecewise polynomial (in this case of degree 3) and the smoothness is adjusted by the definition of a roughness penalty λ.

The parameter λ controls the goodness of fit versus smoothness of the estimated function. For small values of λ, the estimated function $BCS(t)$ adjusts the data as well as possible by reducing the squared error (first part of Equation 5). For larger values of λ, the second derivative (second part of Equation 5) is penalized and which leads to small curvature of the function $BCS(t)$.

Ben Abdelkrim and collaborators provided detailed explanations of the method applied on both body weight and lactation curves (Ben Abdelkrim et al., 2021b). Maximums indicate the beginning of potential deviations from BCS_i^{init} and minimums are the beginning of the recovery period (Fig 2). A limited number of exceptions should be considered if several extremums are present inside a productive cycle, or if there are no extremums, (details of these cases are provided in supplementary hypothesis S1).

Although the procedure determined the beginning and end of the mobilization period t_b and t_e, respectively, existing information on ewes' physiology were also considered for a more reliable estimation of these values. In this respect, t_b can take a value approximately between mating and lambing days, and t_e can take a value approximately between lambing and post-weaning as defined in (Macé et al., 2018). In the construction of PhenoBR, the recovery period of each productive cycle i is over when the next productive period starts $(t = t_b^{i+1})$. A major challenge was then to determine the recovery period when second or third productive cycles were missing for individuals from the original database. For this, it was assumed that in the absence of t_b^{i+1}, the recovery from the productive cycle i would be over 150 days after the post-weaning period (i.e. the period corresponding to the next mating).

This procedure allowed the number of productive cycles and the associated t_b and t_e to be determined for each animal. All missing values of BCS were replaced by values of the function $BCS(t)$. Fig 2 illustrates the perturbation periods as determined by the data analysis procedure against a reproductive cycle as reported in the original dataset. Table 1 summarizes all parameters of the model. The software R version 3.4.2 (R Core Team, 2017) was used for the development of PhenoBR, estimation of the model parameters (function 'optim' of package stat) and for the data analysis procedure (package FDA). The structural identifiability of dynamic model (3) for variables k_b^i and k_p^i was tested using the software DAISY (Bellu et al., 2007), *i.e.* it is possible to estimate uniquely these parameters given the available BCS measurements (Muñoz-Tamayo et al., 2018).

Statistical analysis

Since slight deviations from normality were observed for model parameters (k_b^i, k_p^i and ΔT^i), Spearman correlation test was used to calculate the correlation among model parameters. Analyses of variance were carried out, considering the repeated measures, with the MIXED procedure of SAS (version 9.4; SAS Institute Inc., Cary, NC), considering the repeated measures to test relevant effects and interactions affecting k_b^i, k_p^i and ΔT^i (supplementary code S1). Fixed effects with p<0.05 were considered as statistically significant. Age at first lambing, parity of the ewe, litter size and year of measurement were identified as fixed effects. The age at first lambing effect is the age at which ewes lambed for the first time (i.e. 1 or 2 years; classes 1 and 2, respectively). The parity effect considered first, second and third lambing (i.e. classes 1, 2 and 3, respectively). The litter size effect considered the number of lambs born and suckled by the ewe (i.e. singletons lambed and suckled for class 1; twins lambed but only one suckled for class 2; twins lambed and suckled for class 3 and more than two lambs lambed and suckled for class 4). The first-order interactions between productive cycle and litter size, and between age at first lambing and litter size were tested. The MIXED procedure was used also to compare the parameters k_b^i, k_p^i and ΔT^i for the different BR clusters. Cluster analyses had been previously performed to investigate the variability of BCS profiles during each productive cycle (Macé et al., 2019). Briefly, a functional principal component analysis was performed on individual smoothed BCS profiles to obtain the estimated PC scores. Then, an unsupervised classification was performed. The number of clusters was determined using Akaike and Bayesian information criteria (two to seven clusters were tested). For each productive cycle, models included the cluster factor together with age at first lambing, litter size and the year factors when needed.

To make the model easily usable by non-modellers, PhenoBR is also available as a web interface on the free platform Heroku (http://adaptive-capacity.herokuapp.com/). The web interface was developed using Python 3.7 (Van Rossum and Drake Jr, 1995).

Results

The PhenoBR fitting procedure to estimate parameters k_b^i and k_p^i converged for the 1474 ewes in this study (f_{obj} = 0.54±0.22 units of BCS, Equation 4). Four ewes with only one parity and less than four datapoints were removed, due to insufficient data for estimation of model parameters. The minimum and maximum of the residuals were 0.06 and 1.35 units of BCS, respectively (supplementary figure S1). The dataset used in this study contained ewes with different number of parities (from 1 to 3). To minimize the intervention of the user, PhenoBR enabled us to identify automatically the number of reproductive cycles per ewe (1, 2 or 3), and in each cycle to detect the time of the beginning t_b^i, and the length of the BR mobilization periods ΔT^i (ΔT^1=212.3±51.0, ΔT^2 =174.6±53.4, ΔT^3=181.1±50.2 days). Descriptive statistics of parameters estimated by the model are presented in Table 2. Statistically significant positive correlations were found between parameters of BR mobilization ($p < .001$, $k_p^i, i = 1{,}2\ \ \rho = .6$; $i = 1{,}3\ \rho = .5\ and\ i = 2{,}3\ \ \rho = .5$ for $n = 1478$). Positive and significant correlations between the BR mobilization rate (k_p^i) and BR accretion rate (k_b^i) were observed for parities 1 and 2 ($i = 1, p < .001\ \ , \rho = .4\ ; i = 2, p < .001, \rho = .3$ for $n = 1478$). Statistically significant negative correlations between BR mobilization length ΔT^i and rate k_p^i could also be observed for parities 1 and 3, i.e. the longer the BR mobilization period, the lower the BR mobilization rate (Fig 3; details with scatter plots are provided in supplementary Figure S2). Results of the sensitivity analysis showed that the BCS variance is mainly explained by the parameter k_p during the mobilization period, and by the parameter k_b during the recovery period. This was expected given the structure of the model in which the mobilization and recovery capacity is described by k_p and k_b, respectively.

Parameters k_b, k_p and ΔT were analysed for the effect of productive cycle, litter size, age at first lambing and the year of BCS measurements (Table 3). Analysis of model residuals are presented in supplementary Figures S3 to S6. Even if slight deviations from normality were observed in model residuals, the large number of the sample under study enabled relaxing the normality hypotheses of the residuals (Pek et al., 2018). Statistically significant effects of cycle, litter size and age at first lambing were observed for k_b and k_p. Values of ΔT were affected by the productive cycle and the litter size. A decrease was observed for k_p and k_b, as productive cycle increased. Ewes had the longest period of BR mobilization ΔT at productive cycle 1 and the shortest ΔT at productive cycle 2. As the litter size increased, k_p and ΔT increased and k_b decreased. Ewes that lambed for the first time at age one year showed lower k_b and k_p than ewes lambing for the first time at age 2 years old. The interaction between productive cycle and age of the ewes at first lambing could not be tested owing to uneven distribution of ewes in the classes of each factor. Therefore, the effect of the productive cycle was studied for each class of the age of ewes at first lambing (supplementary Tables S2 and S3). Results showed similar effects of productive cycle to those described above except for statistically non-significant effect of productive cycle on k_b in ewes lambing at age one year old.

A previous study (Macé et al., 2019), using the ewes involved in the present study, showed that ewes' BCS variations could be characterized by three classes of trajectory for each productive cycle (graphs of different clusters are provided in supplementary Figure S7). Ewes with similar trajectories belonged to the same cluster. Major characteristics of these BCS trajectories including BCS level, BCS loss and gain are given in Table 4 based on previous results reported by Macé et al. (2019). The first productive cycle was characterized by clusters BC1, BC2 and BC3, the second by clusters BC4, BC5 and BC6 and the third by clusters BC7, BC8 and BC9. The two major clusters at production cycles 1 and 2 included 99% and 85% of the ewes, respectively (clusters BC1, 63%; BC2, 36% and BC4, 55%; BC5, 30% respectively). In production cycle 3, the major cluster (BC7) included 76% of ewes (BC8, 13%; BC9,11%).

Table 4 summarizes the differences in k_b, k_p and ΔT between clusters at each productive cycle. A statistically significant effect ($p < 0.01$) of clusters was observed for k_p at all three parities. For parameter k_b, the effect of clusters was statistically significant at parities 1 and 3. Finally, only the clusters of parity 1 had a statistically significant effect on parameter ΔT. The value of k_p was higher for ewes in BC3 at productive cycle 1, which is associated with ewes showing a marked and faster loss of body condition at the beginning of the BR mobilization period, compared to ewes in clusters BC1 and BC2. Values of k_b were higher in ewes belonging to BC1 and BC3 at productive cycle 1, clusters associated with ewes showing higher BR restoring capacity, compared to ewes in BC2. During the second productive cycle, a large difference in k_b was observed between BC5 and BC6. Cluster BC6 was associated with ewes showing the highest BR restoring capacity in the shortest lapse of time, and BC5 was associated with ewes that restored less BR in a longer period. During the third productive cycle, k_p was higher for BC9 and BC7, two clusters with ewes with similar BR dynamics characterized by a marked BR loss. The value of k_b was higher for cluster BC8 corresponding to ewes with the highest BCS levels throughout the third productive cycle.

Discussion

The aim of the present study was to propose a metric of ewes' capacity to adapt to their increasing and fluctuating energy requirements through several productive cycles. We exploited the existing database derived from historical and dynamic measurements of BCS in reproductive Romane meat ewes reared in an INRAE experimental farm in France to develop a mathematical model, called PhenoBR. This model converts the individual time series data of BCS into a small number of biologically meaningful synthetic parameters to characterize body reserve dynamics of ewes. Overall and individual body reserve trajectories had been previously described but without characterizing the individual capacity of ewes for BR mobilization and accretion (González-García et al., 2014; Macé et al., 2018). The model developed in the present study characterized each productive cycle i with four parameters specific to each ewe: the BR accretion rate k_b^i, the BR mobilization rate k_p^i, the onset of the mobilization (i.e. onset of the perturbation period) t_b^i and BR mobilization duration ΔT^i. These parameters, never described before, have the potential to offer new indicators of BR dynamics in meat sheep and potentially in other ruminants. The BR mobilization duration (ΔT^i), estimated in the present study, was consistent with previous results and biological knowledge showing that BR mobilization lasted approximately 180 days in our experimental conditions (i.e., almost 90 days in pregnancy and 90 days in suckling; Macé et al. 2018; 2019).

Although in this study subcutaneous adipose tissue, through values of BCS, was used to illustrate the variations in BRs, it is well known that ewes have other sources of energy stored in their anatomy in the form of adipose tissues (e.g. around internal organs, omental, perirenal, inter- or intra-muscular tissues, etc.). Some breeds of sheep present also a specificity to have a fat tail constituting an additional source of energy (Atti et al., 2004). This diversity of adipose tissue sources (locations) can be mobilized in NEB situations (Chilliard et al., 1998). Variations in the magnitude of lipid storage in such mostly internal adipose tissues are undetectable by the BCS, which indicates only the status of the subcutaneous fat layer depth. Therefore, when analysing the energy balance status of a given animal, caution must be exercised when interpreting results from BCS alone, as BR mobilization may be in play without a clear change in BCS. However, subcutaneous adipose tissue is considered as the adipose tissue of most interest for investigating BR changes in ruminants since it is reported to be the most labile adipose tissue, and BCS is closely correlated to total body fat content (Russel et al., 1969). Thus the variables we propose in this study can be considered of high relevance for BR dynamic characterization. Caution should be taken for the use of variables quantified with PhenoBR for other adipose tissues than subcutaneous tissue because both absolute contribution of different adipose tissues to total fat and their relative priority to be mobilised have to be considered (Atti et al., 2004).

Moreover, considering the subjective nature of the body condition scoring, determining both the repeatability and reproducibility (i.e. intra and inter-assessor repeatability, respectively) of BCS measurements is important (Vasseur et al., 2013). In the case of PhenoBR, establishing individual BR trajectories over successive physiological stages required a high level of agreement with fine increments in the grid use to score BCS (0.25 points or lower). Insufficient quality of BCS assessment will limit the detection of slight changes in BR over time. However, this problem could be surpassed in the future by using automatic assessment techniques, such as ultrasound tools.

Several models have been developed for converting time-series data into biologically meaningful variables (Sadoul et al., 2015; Friggens et al., 2016; Nguyen-Ba et al., 2020; Ben Abdelkrim et al., 2021a). Some authors have proposed converting the longitudinal data (such as BW, milk yield and BCS) of dairy goats into small number of variables, using a mechanistic model describing priorities of dairy goats throughout their lifespan (Tedeschi et al., 2013; Puillet and Martin, 2017). Other models have characterized animal responses to different types of perturbations with approaches mainly based on data (Codrea et al., 2011). The objective of all these models was to detect perturbations that affect animal performance and health, and to characterize the animals' responses during such periods. When BCS data were available with high frequency, the models were able to detect and characterize the deviations in BCS due to NEB in early lactation. The originality of PhenoBR compared to the existing models is its use of a combination of a data-driven model (via FDA) and a dynamic model to detect perturbation periods despite the limited number of available BCS records, and to subsequently characterize ewe's response. Using the data analysis approach by FDA helped to decrease the number of variables to be estimated for the dynamic model and thereby increase the robustness of the parameter estimation process (convergence of the process for all animals).

Several biological factors had a statistically significant effect on k_b^i,k_p^i and ΔT^i and were similar to those affecting BCS when considered at a single time-point (Clawson et al., 1991; Marıa and Ascaso, 1999; González-García et al., 2014, 2015). The decrease observed for BR mobilization rate k_p and BR accretion rate k_b (Table 3) as the parity increased, indicates that body condition losses were more marked at the first productive cycle during the BR mobilization period and gained more during the BR accretion period, compared to productive cycles 2 and 3. However, results showed that for ewes lambing at age one year old (supplementary Table S2), the effect of parity on their recovery capacity k_b was not statistically significant. Given that they decrease their k_p as their parity increased, better performance in ewes lambing at an earlier age could be expected.

According to BR mobilization and accretion rates, younger ewes at first lambing lost less body condition and recovered at a lower rate than older ewes. This may be linked to the fact that ewes at age one year are still growing and allocate less energy to adipose tissues to continue their growth and assure their next reproduction cycle. The "round" nature of such growth in younger ewes could induce biases in the BCS assessment as during palpation of the dorsal region, the operator may recognize a larger and confounded mass of muscle and adipose tissues. This is likely the case for the first BCS point in one part of our ewes present in the database (supplementary Table S2 and S3) for which the first BCS could be overestimated in comparison with the same BCS or energy balance status in the following parities. The slope between this first BCS value before mating and the following may be biased, which could affect k_p results in our model (i.e. most drastic BCS variation).

Our results are consistent with those reported by Macé et al. (2018) showing similar effects of parity and age at first lambing when considering BCS changes between successive physiological stages. The BR mobilization and accretion rates estimated in the present study indicated that ewes were able to mobilize more BR as litter size increased, while the BR accretion was less marked for ewes with larger litter size. The increase in BR mobilization rate was expected because of the classical related higher energy requirements for ewes suckling multiple litters. Similar effects of litter size on BR losses during pregnancy and suckling had been previously reported when considering BCS differences between some physiological stages (Walkom et al., 2014; González-García et al., 2014, 2015; Macé et al., 2018). However, the decrease in BR accretion rate with the increase in litter size conflicted with previous results showing higher BR accretion in ewes with higher litter size (Macé et al., 2018). This discrepancy may be related to the fact that in the modelling, BR accretion starts from the beginning of the perturbation, i.e. BR accretion rate was not only considered in the recovery period but also during the theoretical perturbation period in which short anabolic and catabolic reactions could be encompassed.

Positive correlations were found for BR mobilization rates (k_p) between parities, suggesting that ewes maintained their biological capacity for BR mobilization across productive cycles. However, correlations between parities for the other two parameters $(k_b^i, \Delta T^i)$ suggested that BR accretion rate and BR mobilization duration varied across productive cycles. This could be due to higher environmental effects of each cycle (i.e. feed availability, number of lambs previously suckled, etc.) on BR accretion rate and BR mobilization time. Correlations were also found between BR mobilization rate and BR accretion rate suggesting both processes are biologically linked as previously claimed by Chilliard et al. (1998). This result was consistent with high genetic correlations found previously between BR mobilization and accretion in the same dataset, which indicated that ewes exhibiting high level of BR mobilization also exhibited high level of BR accretion (Macé et al., 2018).

The variability in BCS profiles throughout ewes' lifespan had already been investigated by the presence of clusters in each productive cycle (Macé et al., 2019). Each of these clusters were characterized by BR trajectories differing in the level of BR and/or shape of BR changes through the productive cycle. In the present results, we found consistency between average values of BR mobilization and accretion rates and characteristics of BR profiles in clusters. Differences between clusters found in the present study for BR accretion rate k_b and BR mobilization rate k_p suggest that such parameters could be used for ranking animals according to their BR dynamics. Thus PhenoBR offers an opportunity to investigate ewes' variability of response at the individual level.

Perspectives

Farmers and advisers could use the average parameters quantified with PhenoBR to improve and optimize feeding strategies and management at the flock level. For example, BR losses or gains could be converted into energy units, for assessing energy balance at the individual or flock levels. Thus, the feeding system of the flock could be adjusted to improve the BR accretion or BR mobilization considering the physiological stage and different management priorities. In addition, the existing inter-individual variability for BR mobilization and accretion rates and duration of BR mobilization makes these parameters useful for ranking individuals according to their BR dynamics. Such ranking helps at identifying extreme animals for BR management compared to the average of the flock. Combined with their production performances, this ranking contributes to the decision of keeping or culling animals. Furthermore, combination of the individual characterisation of animals with PhenoBR helps geneticists to select animals with better adjustment of BR dynamics to energy requirements. Considering these new criteria for BR dynamics in the breeding objectives enables animal breeding programs to refine selection strategies for more resilient animals. Combining these traits with metabolic data, associated with BCS and therefore with the BR mobilization and accretion processes, will enhance our understanding of mechanisms underlying animal response to NEB perturbations. Altogether, in the perspective of developing resilient farming systems, PhenoBR could help in taking advantage of ruminants' adaptive capacities when facing successive NEB periods or other environmental perturbations affecting nutrient availability and nutritional balances.

Ethics approval

This study was conducted without carrying out any additional animal experiments or biological sampling. The phenotypes used in the present study had been collected previously in other projects that fully complied with applicable legislation on research on animals in accordance with the European Union Council directive (2010/63/EU). All the experimental procedures were performed according to the guidelines for the care and use of experimental animals and were approved by the local ethics committee (approval number APAFIS4597-2016031819254696).

Data and model availability statement

The R script of ODE model and the dataset used for this study are available in public repository Zenodo (http://doi.org/10.5281/zenodo.4300412). The web interface is freely available on http://adaptive-capacity.herokuapp.com/ .

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Author contributions

E.G. and D.H. designed the study and contributed to produce the database used in the current work. M.T. and T.M. developed the model and data analysis procedures. G.K. and M.T. developed the web interface. M.T drafted the manuscript. All authors contributed to the analysis and interpretation of the results. All authors read and approved the final manuscript.

Declaration of interest

The authors declare that they have no competing interests.

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Table 1. Definition of different parameters and constants used in the PhenoBR model to describe the dynamic of BCS for ewes.

Model parameters	**Definition**	**Unit**	**Value**
k_b^i	Rate of BR accretion during the perturbation and the recovery period of productive cycle i	1/ day	Estimation of the model
k_p^i	Rate of BR mobilization during the perturbation of productive cycle i	1/ day	Estimation of the model
t_b^i	Beginning of the perturbation in the productive cycle i	day	Estimation of the model
ΔT^i	Length of the BR mobilization period in the perturbation of productive cycle i	day	Estimation of the model

P_m	Maximum decrease due to the perturbation	Unit of BCS	2
BCS_m	Expected value of BCS in the absence of all perturbation	Unit of BCS	3.5 or 4 depending on the value of BCS_{max}
BCS_{max}	Maximum value of observed BCS for an animal	Unit of BCS	Determined individually from BCS records

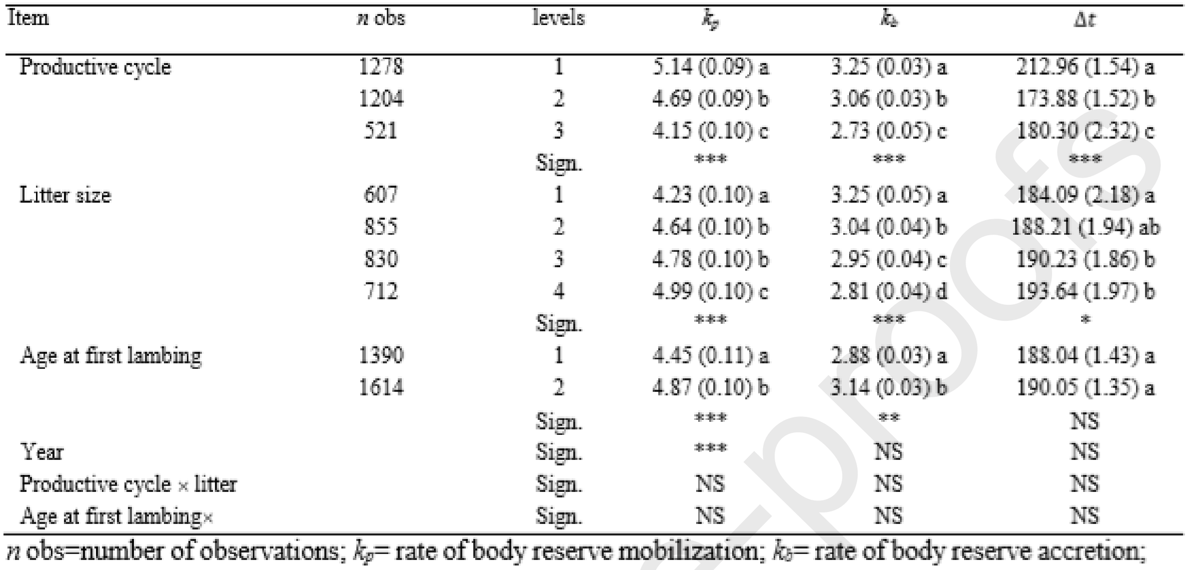
BCS= Body condition score; BR=Body reserves

Table 2. Descriptive statistics of PhenoBR parameters estimated using ewe data.

Item	k_b^1	k_b^2	k_b^3	k_p^1	k_p^2	k_p^3	ΔT_1	ΔT_2	ΔT_3	f_{obj}
Mean	3.296	3.051	2.870	4.979	4.788	4.847	212.3	174.6	181.8	0.537
SD	1.034	1.110	1.078	1.704	1.661	1.401	50.9	53.4	50.2	0.222
Min	0.000	0.000	0.000	1.066	0.000	1.392	34.0	41.0	63.0	0.059
Max	7.755	8.548	8.613	14.349	16.485	10.494	341.0	338.0	372.0	1.355
1st quantile	2.458	2.249	2.257	3.521	3.428	3.859	174.2	135.0	144.0	0.371
3rd quantile	4.038	3.663	3.413	6.161	5.875	5.573	251.0	202.0	214.0	0.691

BCS= Body condition score; BR, Body reserves. k_b^i = accretion rate for the productive cycle ; k_p^i = BR mobilization rate during the productive cycle i of ewes. Parameters k_b^i, and k_p^i are all multiplied by a factor of 1000 for clarity. Parameter $\Delta T_i = t_e^i - t_b^i$ shows the duration of the BR mobilization period at each productive cycle *i*. The quality of model fitness is shown by $f_{obj} = \sqrt{\Sigma_{j=1}^{N}[BCS_j - y(t_j)]^2}$which represents the residual standard error of the model.

Table 3. Summary of least-square means for the model variables (SE) according to the productive cycle, litter size and age of the ewe at first lambing

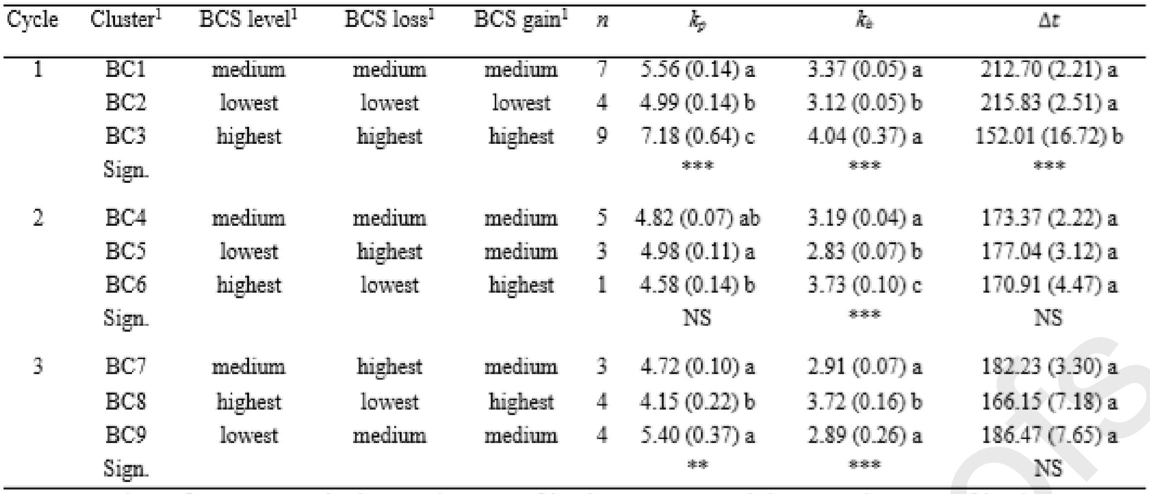


Item	*n* obs	levels	k_p	k_b	Δt
Productive cycle	1278	1	5.14 (0.09) a	3.25 (0.03) a	212.96 (1.54) a
	1204	2	4.69 (0.09) b	3.06 (0.03) b	173.88 (1.52) b
	521	3	4.15 (0.10) c	2.73 (0.05) c	180.30 (2.32) c
		Sign.	***	***	***
Litter size	607	1	4.23 (0.10) a	3.25 (0.05) a	184.09 (2.18) a
	855	2	4.64 (0.10) b	3.04 (0.04) b	188.21 (1.94) ab
	830	3	4.78 (0.10) b	2.95 (0.04) c	190.23 (1.86) b
	712	4	4.99 (0.10) c	2.81 (0.04) d	193.64 (1.97) b
		Sign.	***	***	*
Age at first lambing	1390	1	4.45 (0.11) a	2.88 (0.03) a	188.04 (1.43) a
	1614	2	4.87 (0.10) b	3.14 (0.03) b	190.05 (1.35) a
		Sign.	***	**	NS
Year		Sign.	***	NS	NS
Productive cycle × litter		Sign.	NS	NS	NS
Age at first lambing×		Sign.	NS	NS	NS

n obs=number of observations; k_p= rate of body reserve mobilization; k_b= rate of body reserve accretion;

Δt= duration of body reserve mobilization period; Sign= significance; NS= non-significant. *p*-value= *** <0.001, ** <0.01, *<0.05. Values of least-square means with different letters indicate significant differences between levels of each factor.

Table 4. Summary of least-square means for the model parameters (SE) according to clusters of ewes at each productive cycle.



Cycle	Cluster[1]	BCS level[1]	BCS loss[1]	BCS gain[1]	n	k_p	k_b	Δt
1	BC1	medium	medium	medium	7	5.56 (0.14) a	3.37 (0.05) a	212.70 (2.21) a
	BC2	lowest	lowest	lowest	4	4.99 (0.14) b	3.12 (0.05) b	215.83 (2.51) a
	BC3	highest	highest	highest	9	7.18 (0.64) c	4.04 (0.37) a	152.01 (16.72) b
	Sign.					***	***	***
2	BC4	medium	medium	medium	5	4.82 (0.07) ab	3.19 (0.04) a	173.37 (2.22) a
	BC5	lowest	highest	medium	3	4.98 (0.11) a	2.83 (0.07) b	177.04 (3.12) a
	BC6	highest	lowest	highest	1	4.58 (0.14) b	3.73 (0.10) c	170.91 (4.47) a
	Sign.					NS	***	NS
3	BC7	medium	highest	medium	3	4.72 (0.10) a	2.91 (0.07) a	182.23 (3.30) a
	BC8	highest	lowest	highest	4	4.15 (0.22) b	3.72 (0.16) b	166.15 (7.18) a
	BC9	lowest	medium	medium	4	5.40 (0.37) a	2.89 (0.26) a	186.47 (7.65) a
	Sign.					**	***	NS

n = number of ewes in each cluster; k_p=rate of body reserves mobilisation; k_b= rate of body reserves accretion; Δt=duration of body reserves mobilization period; Sign= significance; NS= non-significant; BC=body condition; BCS= body condition score. p-value= *** <0.001, ** <0.01.

Values of least-square means with different letters indicate significant differences between clusters within a cycle.

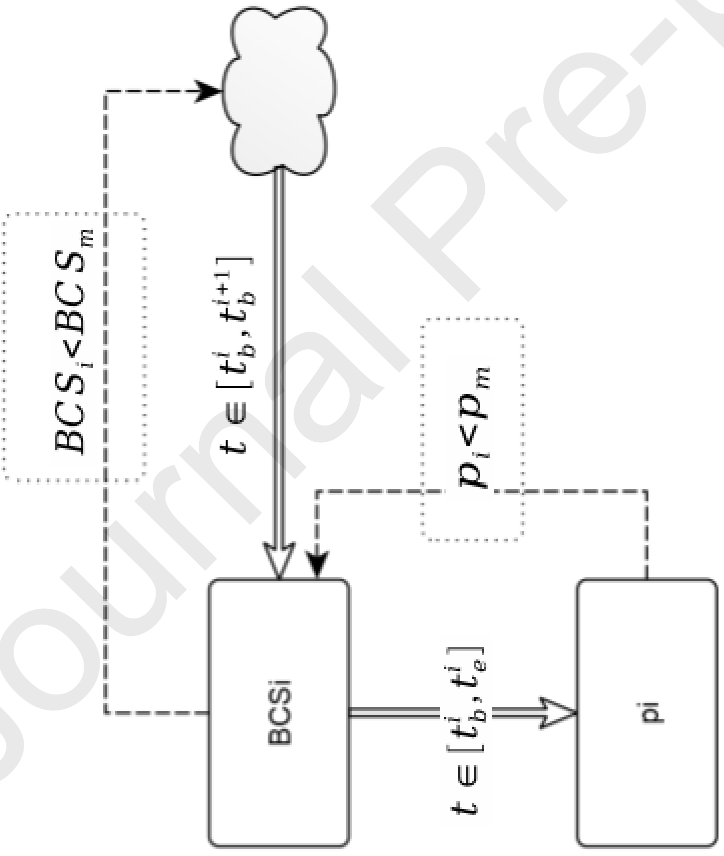
[1] Distribution of ewes in clusters and characteristics of body condition score (BCS) trajectories throughout their productive cycle based on previous results reported by Macé et al. (Macé et al., 2018)

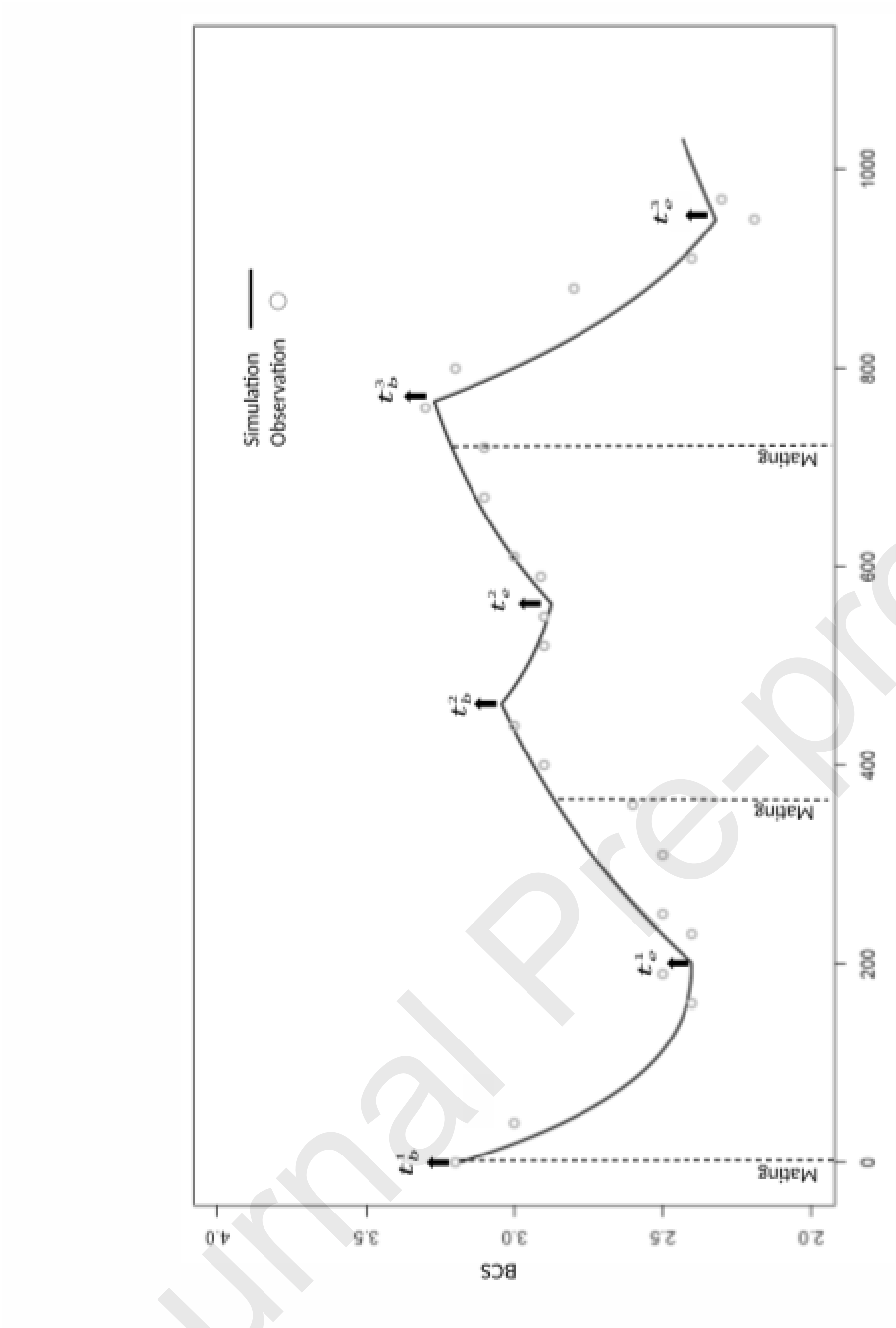
Fig 1. The model for ewe's one productive cycle. Flux to BCS is regulated by the difference between BCS_i and the BCS_m for a given animal. The flux to p_i is activated in the interval $\left[t_b^i, t_e^i\right]$ and will stop when it reaches p_m. From the beginning of the perturbation, the decrease in BCS_i is counterbalanced by all internal physiological mechanisms of the ewes seeking to keep the BCS_i close to BCS_m. BCS_i= variations in BCS during the productive cycle i; pi = decrease in BCS during the mobilization period; BCS= Body condition score; t_b^i = time of the beginning of perturbation; t_e^i = time of the end of perturbation ; p_m= maximal loss of BCS due to a perturbation ; BCS_m= expected value of BCS_i .

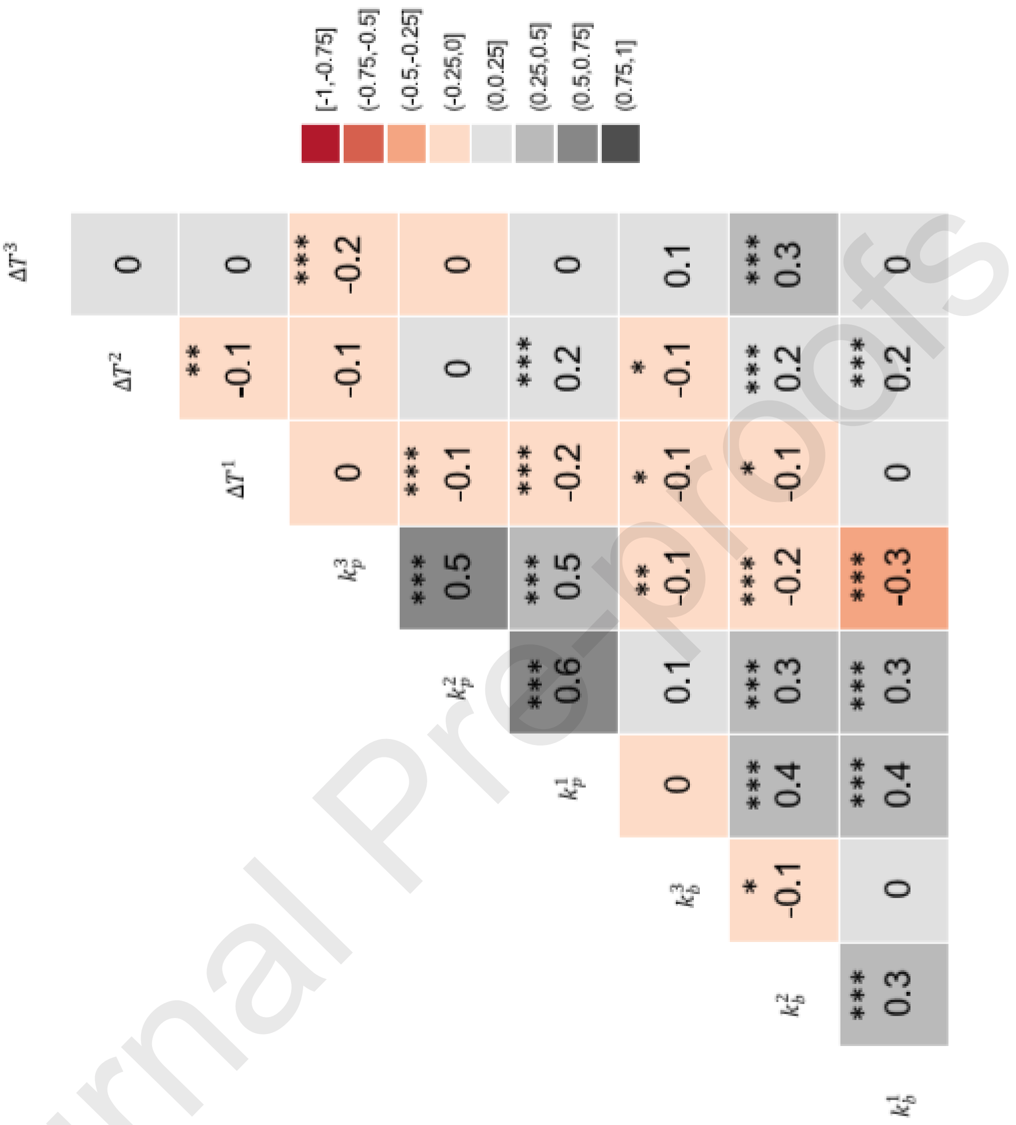
Fig 2. Illustration, for one ewe, of the perturbation periods as determined by the data analysis procedure. Dashed lines show the mating days of each parity as written in the original data set. Time zero represents the first BCS measurement. BCS= Body condition score; . t_b^i = time of the beginning of perturbation i; t_e^i = time of the end of perturbation i.

Fig 3. Correlations between variables k_p, k_b and ΔT as estimated by PhenoBR for ewes' data set used in this study. Grey and red shades stand for positive and negative correlations, respectively. All correlation coefficients and p-values are noted. p-value= *** < 0.001, ** < 0.01, * <0.05. k_p= the rates for BR accretion; k_b= the rates for BR mobilization; ΔT = interval of the perturbation; BR= Body Reserves.

- Body energy reserves are the main source of energy in ruminants facing negative energy balance.
- In situations of negative energy balances, the flexibility of ewes body reserves is of major importance in the current context of breeding for resilience.
- PhenoBR is a model to quantify the body condition score flexibility at individual level.
- PhenoBR contributes to better adapting feeding systems to the individual characteristics of animal.
- PhenoBR helps geneticists to develop animal breeding programs for more resilient animals by including body reserves dynamics.




Simulation
Observation
t_b^1
t_e^1
t_b^2
t_e^2
t_b^3
t_e^3
Mating
Mating
Mating
BCS
2.0
2.5
3.0
3.5
4.0
Days
0
200
400
600
800
1000



	ΔT^2	ΔT^1	k_p^3	k_p^2	k_p^1	k_b^3	k_b^2	k_b^1
ΔT^3	0	0	*** -0.2	0	0	0.1	*** 0.3	0
ΔT^2		** -0.1	-0.1	0	*** 0.2	* -0.1	*** 0.2	*** 0.2
ΔT^1			0	*** -0.1	*** -0.2	* -0.1	* -0.1	0
k_p^3				*** 0.5	*** 0.5	** -0.1	*** -0.2	*** -0.3
k_p^2					*** 0.6	0.1	*** 0.3	*** 0.3
k_p^1						0	*** 0.4	*** 0.4
k_b^3							* -0.1	0
k_b^2								*** 0.3