A dynamic model as a tool to describe the variability of lifetime body weight trajectories in livestock females¹

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ABSTRACT: Until now, the development of precision livestock farming has been largely based on data acquisition automation. The future challenge is to develop interpretative tools to capitalize on high-throughput raw data and to generate benchmarks for phenotypic traits. We developed a dynamic model of female BW that converts BW time series into a vector of biologically meaningful parameters. The model is based on a first submodel that split a female's weight into elementary mass changes related to biological functions: growth (G component), reserves balance (R component), uterine load (U component), and maternal investment (M component). These elementary weight components are linked to the second submodel, which represents the litter developmental stages (oocyte, fetus, neonate, and juvenile) that drive elementary components of dam weight over each reproductive cycle. The so-called GRUM model is based on ordinary differential equations and laws of mass action.

Input data are BW measures, age, and litter weight at birth for each parturition. Outputs of the fitting procedure are a vector of parameters related to each GRUM component and indexed by reproductive cycle. We illustrated the potential application of the model with a case study including growth and successive lactations ($n = 202$) from 45 dairy goats from the Alpine ($n = 27$) and Saanen ($n = 18$) breeds. The fitting procedure converged for all individuals, including goats that went through extended lactations. We analyzed the fitted parameters to quantify breed and parity effects over 4 reproductive cycles. We found significant differences between breeds regarding gestation components (fetal growth and reserves balance). We also found significant differences among reproductive cycles for reserves balance. Although these findings are based on a small sample, they illustrate how use the model can be to adapt herd management and implement grouping strategies to account for individual variability.

Key words: body reserves, dairy female, individual variability, systemic model

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INTRODUCTION

Precision livestock farming (PLF) is a blooming research field, primarily initiated through the automation of data acquisition with electronic devices and computer-based systems for transmitting, warehousing, and processing information (Wathes et al., 2008). Such PLF tools offer potential innovation for farming systems through individual management, and various applications have been tested and already deployed on commercial farms (Halachmi, 2015). For the future,

there is a challenge to design tools to capitalize on the raw data at an individual animal level and produce useful phenotypic information, that is, standardized information synthesizing individual animal performance. Such phenotypic information will contribute to providing quantification of individual variability and benchmarks for decision support.

Regarding livestock females, this challenge is likely to be more difficult because phenotypes exist over a long period of time, imply many regulations over reproductive cycles, and reserves vary with changing physiological stages (growth, gestation, and lactation) and changing environmental conditions (indoor and grazing). Body weight measures are easy to obtain, and in the long term, they provide a life history perspective of the BW trajectory punctuated by the reproductive events, that is, conception

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and parturition. Comparing BW trajectories among females will enable the identification of different types of life history, reflecting how a function is prioritized over others, and the identification of long-term interactions among reproductive cycles, reflecting how early life affects late life. Such understanding of the variability in lifetime performance will be useful to implement adaptive management strategies tailored for a type of trajectory. To make possible the comparison of individual time series between animals, raw data need to be converted into biologically meaningful parameters reflecting lifetime performance over reproductive cycles. Although a number of growth models exist, there is a lack of models that allow the decomposition of lifetime BW trajectories into functional components.

We developed a conversion tool based on the use of a mathematical model designed to be applicable to time series raw data. Contrasting with classical regression models or smoothing methods (e.g., functional data analysis), our approach is based on a purely functional model of the body mass system designed with biologically meaningful parameters. The aim of this paper is to describe the model structure and to illustrate its use with a case study on dairy goats.

MATERIALS AND METHODS

Model Overview, Concepts, and Design

The objective of the model is to translate individual time series of BW raw data into biologically meaningful parameters, quantifying the decomposition of the BW trajectory into functional components. This phenotypic information, that is, a vector of numerical values, enables quantification of differences in the trajectories between individual animals and between reproductive cycles. The model is based on biological concepts with a descriptive objective rather than a predictive one. The female BW trajectory is viewed as the result of various BW changes throughout a lifetime, reflecting investment in various biological functions and associated with changes in reproductive priorities (Martin and Sauvant, 2010; Friggens et al., 2013).

The model combines a BW decomposition submodel at the female level and a reproductive submodel of physiological states over successive reproductive cycles at the level of the offspring, as shown in Fig. 1.

The BW decomposition submodel is based on a systemic view of the female, represented as a generator and regulator of its own body mass and a cyclic procreator of offspring body mass. Changes in BW throughout a lifespan are viewed as resulting from the expression of biological functions. The female weight is represented by a state variable denoted W (g). This variable corresponds

to the current mass of the animal and is altered by the state variables G (g), representing the genetic potential for growth; R (g), representing the balance with the nutritional environment through body reserves between 2 conception events; U_i (g), representing the growth of the gravid uterus (fetuses and annexes: placentome, membranes, and fluids) during the i th gestation; and M (g), representing the change in body reserves during the i th lactation. This so-called GRUM system of variables pertains to virtual masses, reflecting biological functions, which contribute to weight gain and loss by mass exchanges with W through time. The BW is primarily fueled by the genetic potential of growth (G_0 ; g) and increases at constant rate (kG ; g/d) with respect to G_0 . Then, on this genetic-based and long-term weight trajectory, lifetime modulations due to successive reproductive cycles occur. Between reproductive events of the i th reproductive cycle (conception to parturition and parturition to conception), the female BW can change because of the nutritional environment. Apart from BW change induced by gestation or lactation functions, female can gain or lose weight depending on resource availability. This modulation of weight is represented by exchanges with the R component. Between conception and parturition, the female BW is modulated by the gravid uterus load related to the gestation function. The exchange with the U_i component induces a continuous exponential increase during gestation and an instantaneous decrease at parturition. After parturition, during lactation, the female's BW is modulated by the use of body reserves to support the lactation function. This change in BW reflects the maternal investment of the female for the current offspring. At the beginning of lactation, there is a high priority for the current offspring in terms of energy investment, which leads to the mobilization of body reserves. As lactation progresses, the priority for the offspring decreases and allows for the reconstitution of body reserves. This modulation of the female BW is represented by exchanges between W and the M component.

Body mass exchanges between the GRUM components and W are determined by the reproductive cycles, that is, activated or inactivated according to the litter developmental stage.

The reproductive submodel explicitly represents the changes in litter developmental stages during reproductive cycles. Throughout one reproductive cycle, the litter evolves through 4 different successive stages (oocyte, fetus, neonate, and juvenile), represented as compartments through which a dimensionless quantity is flowing (Fig. 2). This theoretical set of compartments is used to formalize the successive activation of each litter developmental stage, which means the activation of specific flows in the BW decomposition submodel. The transitions between stages are triggered by the reproduc-

Figure 1. Diagram of the GRUM model representing lifetime body mass dynamics of livestock females. The model is made of 2 submodels: 1) a female's mass decomposition into a growth component (G), a body reserves balance component (R), a uterus load component during gestation (U_i), and a maternal investment during lactation (M) and 2) a litter developmental stage representation throughout 1 reproductive cycle i , with conception seen as the transition between the oocyte stage (ooc_i) and the fetus stage (fet_i), parturition seen as the transition between the fetus stage and the neonate stage (neo_i), and weaning seen as the transition between the neonate stage and the juvenile stage (juv_i). The conception transition is triggered by date of conception (tc_i) and parturition is triggered by date of parturition (tp_i). dWM_{dep} = mass variation due to reserves depletion in early lactation; dWM_{rep} = mass variation due to reserves repletion in late lactation; dWU_{ges_i} = mass increase due to gravid uterus growth during i th gestation; dWU_{par_i} = mass loss due to litter and placental annexes (placentome, membranes and fluids) expulsion during i th parturition; DWG = mass variation due to growth; DWR = [mass variation due to body reserves balance according to environmental conditions during a reproductive cycle.

tive events occurring during the female's lifespan. The i th conception event leads to a discrete transfer between the compartment ooc_i and fet_i to represent the transition between the oocyte and fetus stages, respectively, that is, the start of the i th reproductive cycle. Then, after a duration corresponding to the gestation length, the i th parturition leads to a discrete transfer between fet_i and neo_i to represent the instantaneous transition between the fetus and neonate stages, respectively. Finally, after parturition and during lactation, the quantity in neo_i is progressively transferred to juv_i to represent the transition between the neonate and juvenile stages, respectively. From the female point of view, this transition corresponds to the transition between maternal energy investments for the current offspring through the lactation function and the maternal energy investment for future offspring through the gestation function (Friggens et al., 2004). In terms of BW modulation, this change in energy investment for biological functions corresponds to a transition between body reserves mobilization and body reserves repletion.

Model Formalism and Assumptions

The model is based on a decomposition of female BW and on litter developmental stages. To reflect elementary exchanges between W and GRUM compo-

Figure 2. Reproductive submodel dynamics during the first reproductive cycle, with conception represented as the transition between the oocyte stage ($ooc[1]$) and the fetus stage ($fet[1]$), parturition represented as the transition between the fetus stage and the neonate stage ($neo[1]$), and weaning represented as the transition between the neonate stage and the juvenile stage ($juv[1]$). The conception event is triggered by the time of first conception in days ($tc[1]$) and the parturition event is triggered by the time of first parturition in days ($tp[1]$).

nents as well as the physiological changes of litter, the formalism is based on ordinary differential equations and laws of mass action. The system of differential equations is described in Table 1 and the model's elements are given in Table 2.

The female's BW is represented by the compartment W (g) with change defined as

$$dW/dt = dW_G + dW_R + dW_{U_i} + dW_{M_i} \quad [1]$$

with t being the time in days and i being an index for the number of the reproductive cycle (i increased to $i + 1$ at each conception).

The mass change associated with the flow dW_G (g/d) represents the genetic-based acquisition of a mature BW due to the animal's own growth during its lifetime. It is defined as

$$dW_G = k_G \times G, \quad [2]$$

with k_G being the growth rate parameter in days^{-1} . The mass change associated with the flow dW_R (g/d) represents the mass change due to body reserve balance according to environmental conditions during a reproductive cycle. It is defined as

$$dW_R = \text{fet}_{i=c} \times k_{rf_{i=c}} + (\text{neo}_{i=c} + \text{juv}_{i=c}) \times k_{rn_{i=c}}, \quad [3]$$

with c (integer) being the number of the current reproductive cycle. Whereas i is the index of reproductive cycles, c is the current reproductive cycle and is used to link the BW decomposition submodel with the reproductive submodel. The parameter k_{rf_i} (d^{-1}) represents the linear mass change rate between the i th conception and the i th parturition. The parameter k_{rn_i} (d^{-1}) represents the linear mass change rate between the i th parturition and the i th + 1 conception. Between the i th conception and the i th parturition, fet_i is equal to 1 whereas neo_i and juv_i are equal to 0; dW_R is determined only by k_{rf_i} . Between the i th parturition and the i th + 1 conception, fet_i is equal to 0 whereas the sum of neo_i and juv_i is equal to 1; dW_R is determined only by k_{rn_i} .

The formalism associated with dW_R is based on the need to give enough flexibility to account for various situations: a female can gain weight ($k_{rf} > 0$) or lose weight ($k_{rf} < 0$) during her gestation, in addition to the mass change due to uterus load, and a female can gain ($k_{rn} > 0$) or lose weight between the body mass at parturition and the body mass at the next conception, in addition to the mass change due to reserves utilization during lactation.

The mass change associated with the flow dW_{U_i} (g/d) represents the BW change related to the gestation function. It is defined as

$$dW_{U_i} = dW_{U_{ges_i}} - dW_{U_{par_i}} \quad [4]$$

The flow $dW_{U_{ges_i}}$ (g/d) represents the mass gain due to gravid uterus growth during the i th gestation and is defined as

$$dW_{U_{ges_i}} = \text{fet}_i \times k_{uf_i} \times (UB_i - U_i) \times \ln \left\{ \frac{[\gamma_1 / (UB_i - U_i)] \times \exp \left\{ \left[\ln (UB_i / \gamma_1) \right] / [1 - \exp(-k_{uf_i} \times \gamma_2)] \right\}}{[1 - \exp(-k_{uf_i} \times \gamma_2)]} \right\} \quad [5]$$

The formalism is based on the Laird model (Laird, 1966) and is used in previous modeling works (Martin and Sauvant, 2010). The parameter k_{uf_i} represents the fetal growth during each i th reproductive cycle, γ_1 (g) and γ_2 (d) are parameters scaling fetal growth, and UB_i is the uterine mass (litter, placenta, and fluids) at parturition of each i th reproductive cycle. The flow is activated by fet_i , which is equal to 1 between conception and parturition. At parturition, fet_i becomes equal to 0, leading to $dW_{U_{ges_i}}$ equal to 0.

The flow $dW_{U_{par_i}}$ (g/d) represents the mass loss due to litter and placental annexes expulsion during the i th parturition and is defined as

$$dW_{U_{par_i}} = (\text{neo}_i + \text{juv}_i) \times 2 \times (UB_i - U_i) \quad [6]$$

The mass change associated with the flow dW_M (g/d) represents the mass change due to body reserves utilization during lactation. It is defined as

$$dW_M = dW_{M_{dep}} - dW_{M_{rep}} \quad [7]$$

The flow $dW_{M_{rep}}$ represents the mass loss due to body reserves depletion at the beginning of lactation and is defined as

$$dW_{M_{dep}} = \text{neo}_{i=c} \times k_{md_{i=c}} \times W, \quad [8]$$

in which k_{md_c} (d^{-1}) is the parameter of body reserves depletion rate for the reproductive cycle i . This flow depends on neo_i , which is equal to 1 at parturition and further decreases to 0 as lactation progresses (transfer to juvi). As a result, $dW_{M_{dep}}$ is high (body reserves are mobilized) in early lactation and decreases to 0 as lactation progresses. In addition, the dynamics of the transfer between neo_i and juv_i (see Table 2) drives the duration of body reserves mobilization (time to BW nadir).

The flow $dW_{M_{rep}}$ represents the mass gain due to body reserves repletion in late lactation and it is defined as

$$dW_{M_{rep}} = k_{mr_{i=c}} \times M, \quad [9]$$

Table 1. Differential system

Variable	Symbol	Differential equation	Initial value	Unit
Maternal weight	W	$dW/dt = dW_G + dW_R + dW_{U_i} + dW_M$	W_0	g
GRUM components				
Growth	G	$dG/dt = -dW_G$	G_0	g
Reserves balance	R	$dR/dt = -dW_R$	0	
Uterine load	U_i	$dU_i/dt = -dW_{U_i} = -dW_{U_{ges_i}} + dW_{U_{par_i}}$	$UB_i - \gamma_1$	g
Maternal investment	M	$dM/dt = -dW_M = -dW_{Mrep} + dW_{Mdep}$	0	g
Litter stages for the i th reproductive cycle				
Oocyte	ooc_i	$dooc_i/dt = -conception_i$	1	1
Fetus	fet_i	$dfet_i/dt = +conception_i - parturition_i$	0	1
Neonate	neo_i	$dneo_i/dt = +parturition_i - weaning_i$	0	1
Juvenile	juv_i	$djuv_i/dt = +weaning_i$	0	1

¹Dimensionless quantity**Table 2.** Variables and flows

Equation	Definition	Unit
Input variables for reproductive cycles $i:1 \rightarrow N$, with N being the maximum number of parturitions achieved by each female		
$t_{P_i} = \{t_{P_1}, \dots, t_{P_{Nmax}}\}$	Parturition times	d
$WB_i = \{WB_1, \dots, WB_{Nmax}\}$	Litter weights at birth	g
Auxiliary variables		
$t_{C_i} = t_{P_i} - \gamma_2$	Conception time of the i th reproductive cycle	d
$c = \text{round}\left[ooc_i + \sum_i (fet_i + neo_i + juv_i)\right]$	Number of the current reproductive cycle	Integer
$SC_i = 0$ if $t \leq t_{C_i}$ or 1 if $t > t_{C_i}$	Conception signal of the i th reproductive cycle	Boolean
$SP_i = 0$ if $t \leq t_{P_i}$ or 1 if $t > t_{P_i}$	Parturition signal of the i th reproductive cycle	Boolean
$UB_i = WB_i \times (1 + k_{ua_i})$	Uterine weight at birth for the i th parturition	g
GRUM flows		
$dW_G = k_G \times G$	Maternal growth	g/d
$dW_R = fet_{i=c} \times k_{rf_{rc}} + (neo_{i=c} + juv_{i=c}) \times k_{m_{rc}}$	Reserve balance	g/d
$dW_{U_{ges_i}} = fet_i \times k_{uf_i} \times (UB_i - U_i) \times \ln\left([\gamma_1 / (UB_i - U_i)] \times \exp\left\{\left[\ln(UB_i / \gamma_1)\right] / \left[1 - \exp(-k_{uf_i} \times \gamma_2)\right]\right\}\right)$	Uterine growth during gestation	g/d
$dW_{U_{par_i}} = (neo_i + juv_i) \times 2 \times (UB_i - U_i)$	Uterine emptying at parturition	g/d
$dW_{Mdep} = neo_{i=c} \times k_{md_{rc}} \times W$	Maternal weight depletion	g/d
$dW_{Mrep} = k_{mf_{rc}} \times M$	Maternal weight repletion	g/d
Litter life stage flows for the i th reproductive cycle		
$conception_i = 5 \times ooc_i \times (fet_i + 0.001 \times SC_i)$	Transition from oocyte to fetus	d ⁻¹
$parturition_i = 5 \times fet_i \times (neo_i + 0.001 \times SP_i)$	Transition from fetus to neonate	d ⁻¹
$weaning_i = k_{n_i} \times neo_i \times (juv_i + 0.001 \times neo_i)$	Transition from neonate to juvenile	d ⁻¹

Figure 3. Illustration of the step-by-step fitting procedure of an individual goat time series BW with adjustment of each GRUM component (G = growth; R = reserves balance; U = uterine load; and M = maternal investment).

in which k_{mr_i} (d^{-1}) is the parameter of body reserves repletion rate. With this formalism, repletion of body reserves is defined as a complete recovery of body reserves lost in early lactation.

The reproductive submodel stands for the litter stages during the reproductive cycles. For the i th reproductive cycle, the oocyte, fetus, neonate, and juvenile stages are represented by 4 compartments: ooc_i , fet_i , neo_i , and juv_i . Each reproductive cycle i is thus individualized by flows between compartments ooc_i , fet_i , neo_i , and juv_i . These flows correspond to the physiological transitions due to conception, parturition, and weaning as shown in Fig. 2. The conception event of the i th reproductive cycle is triggered by the variable t_{c_i} , representing the date of conception in days and leading to a discharge of ooc_i in fet_i . To estimate t_{c_i} , the model uses the date of parturition, t_{p_i} in days, and a gestation length equal to γ_2 , in days. The parturition event is triggered by t_{p_i} and leads to a discharge of fet_i in neo_i . The flows conception and parturition are formalized as instantaneous transfers that mimic discrete shifts in physiological states. In contrast, the weaning flow is represented as a progressive transfer from neo_i to juv_i , which is controlled by the parameter k_{n_i} (d^{-1}) and drives the transition between depletion and repletion of body reserves. The reproductive submodel accounts for all the reproductive cycles of female's lifespan, indexed with i , and the variable c is used to specify the number of the current reproductive cycle to the BW decomposition submodel (see Table 2).

Data and Fitting Procedure

The model was implemented with the ModelMaker 3.0 software (Cherwell Scientific Ltd., Oxford, United Kingdom), using the Runge-Kutta 4 numerical integration procedure and a fixed integration step of 1 d for t ranging from 0 (birth of the female) to the time of the last BW measure. The fitting procedure was performed using the ModelMaker 3.0 optimization package (Cherwell Scientific Ltd.), based on the simplex algorithm, and required as input data the time series of BW measures, age at parturition (t_p), and the litter weight at birth (WB_i) for each i th parturition.

The fitting procedure was performed step by step for each female time series BW, with each component of the GRUM model being fitted in a sequential order as shown in Fig. 3. The first step was to estimate the growth components W_0 and G_0 , defining the initial value of the female weight and the growth potential (as the initial value of G) respectively, and therefore the weight at maturity. Then, the fitting procedure was performed for each reproductive cycle i , with i varying from 1 to N_{max} (the last reproductive cycle with data records).

Model Use: Dairy Goat Case Study

We used data from 45 dairy goats of the experimental herd of the research unit Systemic Modelling Applied to Ruminants (Paris, France) as a case study (see Fig. 4). The females, from the Alpine and Saanen breeds, were born between 2004 and 2009 and were not

Figure 4. Time series of individual BW data ($n = 12,696$ measurements) of the 45 dairy goats used in the case study (dark circles) from birth to culling and their litter weight at birth (gray circles) at each parturition.

involved in experimental treatments that could have altered their BW trajectories. These females also had complete information at each parturition (age and total litter weight for 202 parturitions) and had weekly measurements of BW from birth to culling, giving a total of 12,696 BW measures, as shown in Fig. 3. All females had at least 3 lactations. Five females had extended lactations: because they failed to get pregnant, they were not dried off and, therefore, they waited until the next breeding season. The different types of lifetime profile are described in Appendix 1. After a preliminary test, the parameter k_G was fixed to 0.002 for all the 45 females as W_0 and G_0 were sufficient to represent the variability of all individual growth component G. The parameter k_{mr_i} was also fixed to 0.02 for all reproductive cycle because k_{n_i} was sufficient to represent the variability of all individual reserves repletion components. Finally, the outputs of the fitting procedure for a goat with $N_{\max}$ reproductive cycles are the initial values W_0 and G_0 and $N_{\max} \times 6$ values for GRUM parameters (k_{rf_i} , k_{rn_i} , k_{ua_i} , k_{uf_i} , k_{n_i} , and k_{md_i}).

RESULTS

The fitting procedure converged for the 45 individual BW trajectories included in the analysis. The mean root mean square error was 2.35 kg with a SD of 0.55 kg, a minimum value of 1.45 kg, and a maximum value of 3.63 kg. The distribution of residuals, corresponding to BW measured minus BW predicted,

is presented in Fig. 5. The box plots of the residuals by time intervals of the goat lifetime are presented in Fig. 6. The first and third quartiles of residuals distributions by time interval were -0.96 ± 0.37 and 1.45 ± 0.54 kg, respectively. The model was able to represent a variety of lifetime BW trajectories and particularly trajectories with extended lactations as shown in Fig. 7.

To illustrate the potential of the model to be a tool for quantifying individual variability, we chose to focus on the first 4 reproductive cycles, as the number of goats was not equivalent in all lifetime profiles. For each goat, the fitted parameters constituted a phenotypic vector. The descriptive statistics of the fitted parameters are presented in Table 3. The whole set of individual vectors provides a quantitative view of individual variability: it can be analyzed to assess the parity, breed, or animal effect. Data were analyzed with parameter estimates by cycle considered repeated measures of individual goats, with a first-order autoregressive structure of variance and with a statistical model including fixed effects of breed, cycle, and breed $\times$ cycle interactions (mixed procedure of SAS, version 9.4, 2017; SAS Inst. Inc., Cary, NC).

The growth component G was reflected by W_0 , the weight at birth, and G_0 , the weight at maturity. Regarding the weight at birth, Alpine goats were heavier (4.26 ± 1.1 kg) than Saanen goats (3.70 ± 0.7 kg) but this difference was only slightly significant (see Appendix 2). In contrast, Saanen goats had a higher weight at maturity (110.02 ± 22.1 kg) than Alpine goats (95.18 ± 14.6 kg) and this difference was significant.

The reserves balance component R within a reproductive cycle was reflected by 2 phases of BW change: 1) change of BW from conception to parturition (parameter k_{rf_i}), in addition to BW change due to gestation, and 2) change of BW from parturition to next conception (parameter k_{rn_i}), in addition to BW change due to body reserves use in lactation. For the first phase of the reproductive cycle, both breed and parity had a significant effect on the use of maternal reserves to support the fetus growth (parameter k_{rf_i}). During the first reproductive cycle, females lost weight between conception and parturition ($k_{rf_i} < 0$; Table 3). This BW loss was greater for Saanen goats than for Alpine goats. For the next reproductive cycles, females stopped using reserves to support gestation and gained weight between conception and parturition (increase in value of k_{rf_i} with the number of the reproductive cycle). The BW gain was greater for Alpine goats than for Saanen goats. For the second part of the reproductive cycle, only parity had a significant effect on the BW change between parturition and the next conception (k_{rn_i}). Females lost weight between parturition and the next conception ($k_{rn_i} < 0$). This BW loss decreased when parity increased: as females aged, they lost less BW between parturition and the next conception.

The uterus load component U_i was reflected by the rate of fetal growth (parameter k_{uf_i}) and the ratio of litter weight to gravid uterus weight (parameter k_{ua_i}) during the i th gestation. The fetal growth was significantly influenced by breed and parity. Saanen goats had a greater uterus growth than Alpine goats. The ratio of litter weight to gravid uterus weight was not influenced by breed, but the parity had a significant effect.

The maternal investment component M was reflected by the rate of body reserves depletion (k_{md_i}) and the duration of body reserves depletion (k_{n_i}). The rate of body reserves depletion was not influenced by breed and parity. For the duration of reserves depletion, Saanen goats exhibited a slightly shorter time than Alpine goats.

DISCUSSION

The GRUM model aimed at converting time series BW measurements into biologically meaningful parameters. This conversion is based on a decomposition of female's BW into elementary mass changes that reflect changes in a females' priority for different biological functions throughout their lifespan. With this systemic view of BW trajectory, the outputs of the fitting procedure have a biological meaning. This original feature of our work is complementary to other existing models. Indeed, models have been previously developed for growth (sheep [Soboleva et al., 1999] and cattle [Oltjen et al., 2000]) and for reserves changes during lactation in cattle (Roche et al., 2007; Tedeschi et al.,

Figure 5. Distribution of the residuals ($n = 12,696$) obtained after the fitting procedure of 45 goats' BW trajectories (50% of residuals are between -1.05 kg and $+1.20$ kg).

2013), based on a structural decomposition of BW (e.g., protein, fat). These models are valuable for predictive usage but they are less adapted to our objective of describing an individual lifetime BW trajectory and quantifying how different trajectories are between animals.

The potential of the model of being incorporated as a trajectory generator in a PLF tool was illustrated with a case study on dairy goats. The fitting of 45 individual trajectories provided 2 types of information. First, the model was flexible enough to accommodate various lifetime trajectories, such as those including extended lactation, and, therefore, is adapted to study individual variability. Second, the parameters obtained from the fitting procedure allowed the comparison of individuals regarding their BW, helping the interpretation of frequent time series. In this paper, the case study had only an illustrative purpose but the differences we found between breeds and parities can help to adapt management. For instance, results showed that during the first gestation, females had a negative reserves balance and this was more pronounced for Saanen goats. This information can be used to set up group feeding strategies based on breed and parity and adapt the diet for the group. Although the case study was performed on dairy goats, the GRUM model is generic enough to be applied to various livestock species (cows, ewes, sows, etc.). This model flexibility is grounded in the systemic decomposition of BW trajectory into elementary biological functions common to all mammal females.

Automatic measures of BW are now very common in commercial dairy farms as females are weighed at the milking parlor. Dynamic changes of BW provide very useful information, especially for high-yielding dairy females. Lower body condition in early lactation may lead to reproductive disorders or health problems (Pryce et al., 2001; Roche et al., 2009). Recent work has shown

Figure 6. Box plots of the residuals ($n = 12,696$) by time intervals of the goat lifetime ($n = 45$ goats). Intervals are defined for each goat by t_{Ci} and t_{Pi} , that is, the conception and parturition times, respectively, of the i th reproductive cycle. The size of each box plot is proportional to the number of residuals.

that frequent BW measurements provide an estimation of energy balance and therefore constitute a useful on-farm management tool (Thorup et al., 2013). Before using BW measures as proxies for intrinsic animal traits, it will be necessary to take into account the gut fill to correct BW measures (Thorup et al., 2012). It will also be necessary to track the nutritional environment of females in addition to BW measures to check the consistency of the reserves balance in the model (R component).

A key perspective for the GRUM model is its implementation on large populations of females raised in various environmental conditions. With a high number of animals characterized by a vector of BW parameters, it will be possible to disentangle the relative role

of genetics and environmental effects in BW trajectory variability. Body reserves utilization and, therefore, changes in BW have a genetic basis (Friggens et al., 2013). With statistical approaches such as mixed models, the GRUM outputs can be used to assess the repeatability of BW changes over reproductive cycles. The recent work of Zachut et al. (2017) has shown a consistent pattern of postpartum BW loss in high-yielding cows across lactations. The same type of results was found in rabbit does (Bonachera, 2017). Our model makes it possible to go further because fitted parameters are not only aggregated variables such as BW loss; rather, they reflect the dynamic aspects of BW. In addition to this permanent female effect on BW tra-

Figure 7. Illustration of the BW trajectory (solid line) obtained after the fitting procedure of the GRUM model on the BW time series (circles) of a goat with 6 reproductive cycles and an extended lactation for the fifth cycle.

Table 3. Descriptive statistics of fitted items (initial values W_0 and G_0 or parameters k_{rf} , k_{rn} , k_{ua} , k_{uf} , k_n , and k_{md} with i being the number of the reproductive cycle) with the GRUM model for each breed over the first 4 reproductive cycles (45 individuals for each parameter, except for parameters related to the fourth cycle with 44 individuals)

Fitted item	Mean		SD		Minimum		Maximum	
	ALP ¹	SAA ²	ALP	SAA	ALP	SAA	ALP	SAA
W_0	4,266.3	3,707.0	1,101.8	672.0	1,579.6	2,816.0	6,009.3	4,743.9
G_0	95,186.7	110,242.3	14,600.0	22,065.2	74,360.3	85,607.6	135,463.5	148,841.0
$k_{rn}[1]$	-63.1	-61.7	20.5	27.8	-100.0	-120.0	0.0	-10.0
$k_{rn}[2]$	-45.0	-44.7	20.7	26.1	-85.0	-100.0	-5.0	0.0
$k_{rn}[3]$	-28.5	-26.4	17.1	34.7	-60.0	-80.0	5.0	45.0
$k_{rn}[4]$	-20.4	-28.6	25.1	25.1	-100.0	-70.0	10.0	0.0
$k_{rf}[1]$	-12.6	-23.0	33.4	36.1	-80.0	-105.0	65.0	10.0
$k_{rf}[2]$	17.2	-0.2	22.1	27.9	-20.0	-40.0	70.0	70.0
$k_{rf}[3]$	31.9	13.1	23.0	45.8	-20.0	-100.0	70.0	80.0
$k_{rf}[4]$	48.1	39.4	34.2	24.6	-30.0	0.0	140.0	80.0
$k_{uf}[1]$	0.026	0.032	0.006	0.008	0.021	0.021	0.040	0.040
$k_{uf}[2]$	0.021	0.026	0.005	0.006	0.010	0.021	0.035	0.040
$k_{uf}[3]$	0.025	0.030	0.005	0.011	0.020	0.021	0.035	0.050
$k_{uf}[4]$	0.024	0.025	0.005	0.007	0.021	0.021	0.035	0.040
$k_{ua}[1]$	0.930	0.956	0.296	0.317	0.400	0.400	1.500	1.500
$k_{ua}[2]$	0.748	0.711	0.318	0.194	0.300	0.300	1.800	1.200
$k_{ua}[3]$	0.852	0.844	0.265	0.248	0.300	0.500	1.500	1.400
$k_{ua}[4]$	0.769	0.922	0.304	0.334	0.300	0.500	1.500	1.500
$k_n[1]$	0.189	0.310	0.155	0.183	0.050	0.080	0.500	0.500
$k_n[2]$	0.161	0.210	0.153	0.193	0.020	0.020	0.500	0.500
$k_n[3]$	0.189	0.228	0.175	0.180	0.020	0.050	0.500	0.500
$k_n[4]$	0.240	0.278	0.213	0.192	0.025	0.025	0.500	0.500
$k_{md}[1]$	0.0033	0.0036	0.0009	0.0016	0.0020	0.0030	0.0060	0.0090
$k_{md}[2]$	0.0037	0.0037	0.0022	0.0014	0.0020	0.0020	0.0120	0.0080
$k_{md}[3]$	0.0040	0.0038	0.0035	0.0014	0.0020	0.0030	0.0200	0.0080
$k_{md}[4]$	0.0033	0.0029	0.0010	0.0006	0.0020	0.0020	0.0060	0.0050

¹ALP = Alpine breed.

²SAA = Saanen breed.

jectory, comparing vectors of parameters for animals in different environments (e.g., grazing versus indoor) will provide information on the adaptive capacities of females. Finally, if populations are also characterized in terms of genetics (recording of pedigree or genomic markers), it will possible to compute genetic values of BW parameters, such as breeding values.

The type of systemic model presented here can be extended to other phenotypic measures. Instead of applying purely mathematical decomposition of phenotypic measures, applying systemic modeling can be very useful to analyze high-throughput data because it will provide biologically meaningful parameters, which are easier to interpret for biologists. The field of PLF has made a lot of progress in data acquisition, and now the challenge is to transform data into information.

Furthermore, conversion of time series data related to different biological aspects (behavior, health, intake, etc.) into vectors of parameters will allow multivariate analysis of various phenotypic traits. Such a comprehensive view of animals is essential to deepen our

understanding of complex phenotypes such as feed efficiency or robustness (Friggens et al., 2017), especially for dairy females, where the profiles of body reserves mobilization play a great role in evaluation of the genetic basis of feed efficiency (Berry and Crowley, 2013).

Beyond the scope of extracting biological information from BW trajectories, the GRUM model opens perspective for on-farm management. The objective is to move from an a posteriori prediction to an a priori prediction of BW trajectories. On-farm automation of the fitting procedure can help to anticipate deviations in BW trajectories and prevent associated disorders such as fertility decrease or metabolic disease. Such real-time use of the model will take advantage of the recent development of machine learning methods (Borchers et al., 2017). Analysis of BW trajectories of females currently in the herd will be based on the trajectories collected in the past.

Appendix 1. Description of the lifetime trajectories for the 45 goats used in the case study

Lifetime profile				
Number of reproductive cycles	Number of extended lactations	Alpine goats	Saanen goats	Total
3	0	1		1
4	0	15	12	27
	1	1		1
5	0	4	4	8
	1	2		2
6	0	2	1	3
	1	2		2
7	0		1	1

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Appendix 2. Effects of breed and parity on fitted items from the GRUM model

Parameter	Biological meaning	Effect ¹		
		Breed	Cycle	Breed × cycle
W_0	Birth weight	†	nd	nd
G_0	Mature weight	**	nd	nd
k_{rf}	Prepartum weight change	**	‡	NS
k_{rn}	Postpartum weight change	NS	‡	NS
k_{ua}	Fetal annexes to litter weight ratio	NS	**	NS
k_{uf}	Fetal growth	**	‡	NS
k_n	Reserves depletion duration	†	NS	NS
k_{md}	Reserves depletion rate	NS	NS	NS

¹nd = not determined; NS = nonsignificant.

†*P*-value < 0.1; ***P*-value < 0.01; ‡*P*-value < 0.001.

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