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REPROsheep: A model that integrates individual variability to optimise hormone-free reproduction management strategies for a dairy sheep flock

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ABSTRACT

Managing reproduction of a dairy sheep flock without using hormones for oestrus induction and synchronisation is an alternative method that complies with agroecological principles, animal welfare and public health concerns. However, shifting from conventional reproductive management to a hormone-free philosophy means leaving more room for individual intraflock variability in oestrus occurrence. The success of establishing alternative hormone-free reproduction systems relies on managing the variability of ewes' individual responses, which are themselves influenced by individual characteristics. Therefore, the so-called REPROsheep model was built to study the effects of individual ewes' characteristics, such as age, body condition score (BCS) or milk yield, on individual responses, as well as the overall productive and reproductive performances of the flock. This dynamic agent-based model (ABM) represents individual reproduction and lactation processes in a hormone-free management context. Outputs at the flock level were simulated using this model. Two dynamic outputs (weekly number of ewes lambing and weekly milk yield) and two punctual outputs (total number of ewes lambing and total milk yield) were simulated. Sensitivity analysis showed that the studied outputs were affected by ewe age, pre-mating BCS and milk-yield distributions in the flock. Increasing average age or pre-mating BCS by 0.5 from a starting point of 2.5 and average milk-yield by 50 L from a starting point of 195 L appeared to increase, for one breeding season, the number of ewes lambing, the concentration of those lambing events over one period, as well as total milk yield, whereas decreasing the average value of these factors by the same amount appeared to produce the opposite effect. Management strategies favouring an optimum age and pre-mating BCS, as well as good milk yield for the individuals of the flock, may thus be a lever for optimising performance, especially lambing distribution over time. Therefore, the REPROsheep model seems relevant to determine how a management strategy (affecting flock structure in terms of age, body condition or production potential) can impact the performance of a dairy sheep flock in the context of hormone-free reproduction.

1. Introduction

To achieve agroecological transition goals, French livestock farming systems are expected to maintain their productive performance while responding to a diversity of complex environmental, social and economic challenges. This implies a willingness to design farming systems based on biological regulations, adding value from interactions between the farming system components while enhancing autonomy and self-sufficiency in inputs (Thenard et al., 2014). Reproduction practices are among the practices to be revisited in such a paradigm shift, which is particularly challenging in seasonal species such as sheep. In this regard, alternative sheep farming systems have been conceived, taking into account the emergence of new and serious ethical issues related to animal welfare and public health concerns (Martin et al., 2004). Alternative solutions are investigated to limit hormonal treatments that have been conventionally used to induce and synchronise ovarian cycles in small ruminants (Pellicer-Rubio et al., 2019). The use of photoperiodic treatments or the so-called "male effect" technique are, in fact, functional alternatives to hormonal treatments for stimulation and synchronisation of ewe ovulatory activity (Lurette et al., 2016). However, these alternatives imply leaving more room for individual variability in oestrus occurrence, which suggests that the success of hormone-free

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reproduction at the flock level would rely on managing the variability of individual responses. These individual responses are related to intrinsic characteristics of the ewes as well as to the structure of the flock resulting from the management strategy of the farmer. Factors such as body condition score (BCS) (Russel et al., 1969; Kenyon et al., 2014), age (Fahmy, 1989; Notter, 2000) and production potential (Gootwine and Pollott, 2000) are known to be strongly related to reproductive performance in sheep. Therefore, heterogeneity in flock structure in terms of age distribution, BCS and/or individual production levels is expected to induce variability in individual responses to breeding practices, a key component for understanding flock function (Puillet et al., 2010b).

Flock simulation models are an interesting methodological resource to address this issue because they enable us to improve our ability to predict the responses of a flock to the management practices to which it is subjected (Tichit et al., 2009). The so-called agent-based modelling (ABM) method allows an interesting bottom-up approach in which the emphasis is placed on modelling the agents (entities, in our case sheep and farmer) and the interactions between them and their environment. The global performance of the modelled system then emerges from dynamic interactions between agents and/or their environments (Bruch and Atwell, 2015). We speculate that this agent-based approach will allow us to build a model to evaluate the impacts of individual variability in reproductive responses on the overall performance of a dairy sheep flock managed with alternative practices without hormones. For this, a detailed representation of ovine reproductive processes is required. Some models have been applied to dairy cattle herds (Oltenacu et al., 1980; Brun-Lafleur et al., 2013) to precisely represent both reproductive processes and individual variability. To our knowledge, there is a lack of this kind of model for sheep flocks, particularly for dairy sheep systems. However, some deterministic models are available. They usually represent hormonal management of reproduction and involve fertility rates, fixed for the totality or one part of the flock, by breeding season, by genotype or by age category (Benoit, 1998; Lesnoff, 1999).

A dynamic model incorporating the individuality of ewe reproduction is needed to conceive alternative dairy sheep farms based on new reproductive process management. Therefore, the aim of this work was to build an ABM to help evaluate the effects of using alternative hormone-free reproduction practices in dairy sheep flock management. The model would contribute to a better understanding of the interplay between the variability in the specific traits of individual ewes and their individual and whole flock reproductive performances.

2. Materials and methods

The model was built using GAMA software (Taillandier et al., 2019), which was designed for the development of ABM. The following description is given according to the rules of the O.D.D. protocol (Overview, Design concepts, Details), specifically created for the description of ABM (Grimm et al., 2010).

2.1. REPROsheep: A model to simulate the reproductive dynamics of a hormone-free dairy sheep flock

2.1.1. Purpose

The REPROsheep model was designed to represent the reproductive dynamics in a dairy sheep farm managed without hormonal treatments for induction and synchronisation of ewe oestrus. It took into account the individual variability of oestrus based on a detailed representation of the individual reproductive process. The objective was to understand the extent to which the number of ewes lambing and the milk production over one production season, at the flock level, are influenced by several individual characteristics of dairy ewes (e.g., age, BCS and milk yield level) and their distribution in the flock.

2.1.2. Model baseline and overview

To represent the mechanism of reproduction without hormones and to formalise the link between ewe characteristics and reproductive performance, data available from Debus et al. (2021) were used. This database reports the result of a 5 year experimental monitoring (from 2012 to 2016) of a flock composed of approximately 300 Lacaune ewes (ewe lambs and adult ewes) in an organic farm (i.e., without hormonal treatments) in the Roquefort basin (South France). The studied farm, known as "off-season", was characterised by unseasonal breeding in spring (Fig. 1), different from conventional farms (seasonal) where the animals are bred in mid-summer or early autumn (during their natural breeding season). During the experimental monitoring, the "male effect" (ME) technique was used to induce and synchronise oestrus in the flock without hormonal treatment. This technique consists of introducing, after a separation time of at least one month, a sufficient number of rams into a flock of ewes under seasonal anoestrus (i.e., at sexual rest). This practice induces an almost immediate increase in luteinising hormone (LH) secretion, leading to ovulation and resumption of oestrus cycles within 15 days (Martin et al., 1986; Thimonier et al., 2000). The proportion of ewes responding to ME during anoestrus season have been shown to be highly variable, depending on time of use, breed (Rosa and Bryant, 2002; Chanvallon et al., 2011), age or nutritional status of rams and ewes (Ungerfeld et al., 2004; Maatoug-Ouzini et al., 2013; Alhamada et al., 2017). The depth of anoestrus (i.e the proportion of ewes showing spontaneous ovulation before any synchronisation technique) has also been found to influence the response to ME depending on the breed (Thimonier et al., 2000; Chanvallon et al., 2011). Overall, it has been demonstrated that the response to ME is highly variable and that this variability has many origins and underlying factors which have been studied generally one by one and usually in meat breeds as milking adds supplementary potential impact factors. Debus et al. (2021) studied the simultaneous link between some of the previously cited factors and short term ovarian response of milking Lacaune ewes to the male effect. The available database of their work provided access to individual ewe information concerning pre-mating BCS (BCS, scored one week before introducing the rams for ME), age at breeding time (Age), lactation number ($Lact_{num}$), interval (days) between last lambing and the male effect (LMEI), milk performance (third milk yield monitoring (TDMY, measured a few days before the male effect) and total milk yield from previous lactation (LTMY)) for each ewe (Table 1b), as well as the cyclicity status of each ewe before the male effect (CBME; i.e., in oestrus before the ram was introduced) and its response to the male effect (RME). This information was used to develop the equations used in the model to link all these characteristics of the ewes to their reproductive performance (Section 2.1.7.SM2).

The flock reproduction management that was modelled consisted of separate management strategies for two batches: the adult ewes batch (ewes that have completed at least one lactation) and the ewe lambs batch (young ewes that have never been mated). Only the adult ewes were subjected to off-season ME and were then naturally mated with rams. The ewe lambs were mated for the first time in mid-summer (i.e., close to the natural breeding season) so that ME was not necessary to stimulate their ovarian cycle. Adult ewes that did not respond to the ME in spring were added to the ewe lamb batch for mating in mid-summer without ME. With such management, the lambing period began in early autumn of year 'n', with the milk delivery period running from late October of the same year to August of year 'n + 1' (Fig. 1).

2.1.3. Entities, state variables and scales

Entities: The model presented two main types of entities, i.e., (i) a decision-making or human entity: the farmer, and (ii) biotechnical animal entities: sheep divided into two subentities according to reproductive animal category (or sex): ewes and rams.

State variables and attributes: Tables 1a and 1b describe the main model parameters, state variables and attributes. Fig. 2 provides an overview of the model structure in the form of a unified modelling

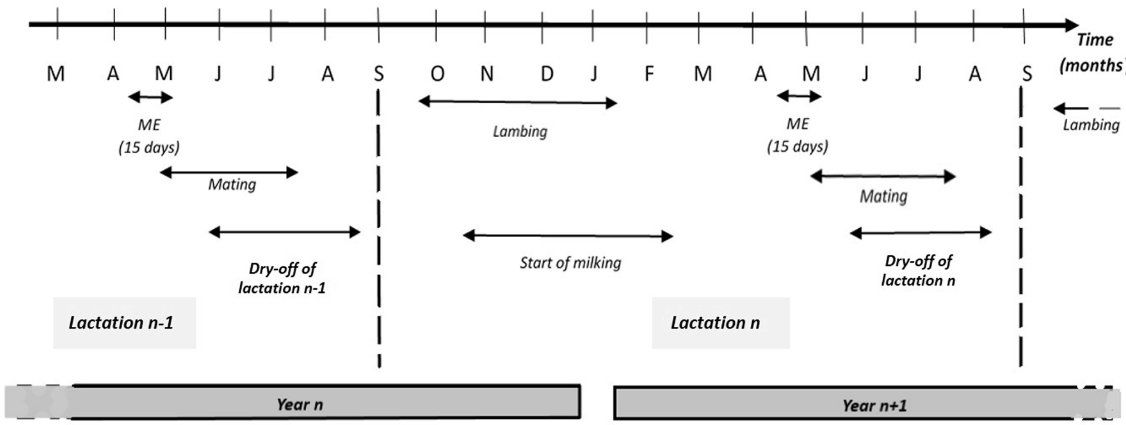

Fig. 1. Organisation of the main steps of reproduction and lactation management over one production season for off-season breeding with one lambing per year. ME: male effect.

Table 1a
Main parameters, attributes and state variables of the REPROsheep model.

Parameters	Definition	Notation	Type	Units	Initial value/ range of values in the model	Source
Starting date of the simulation	–	–	Date	–	04/17/(n)	–
Ending date of the simulation	–	–	Date	–	08/16/(n + 1)	–
Ram introduction date for male effect	Date on which the farmer introduces rams into the flock and leaves them for 15 days (without the possibility to mate) in order to stimulate the ovarian cycle of ewes	–	Date		04/17/(n)	*Experimental data of* Debus et al.(2021)
Probability to be in seasonal oestrus[1]	Probability that the ewe is in a period of heat and will accept mating	Pso	Float[2]	%	80	*Adapted from* Chemineau et al. (1992)
Minimum milk yield accepted at milking	Daily milk production value below which the farmer decides to dry up the ewe	MMYA	Float	L/day	0.8	*Expert criteria*
Probability of abortion	Probability for a pregnant ewe to lose the foetus(es) before term	Pa	Float	%	2	
Probability of an easy lambing	Probability to lamb without complications preventing the milking or leading to a health problem	Pel	Float	%	96	
Probability for a successful mating	Probability for an ewe to become pregnant after mating	Pms	Float	%	50	
Rams introduction date for the mating of ewe lambs and adult latecomers	Date on which the farmer introduces rams to mate young ewes (<1 year old) and the adult ewes that did not get pregnant during the previous mating period	–	Date		07/15/(n)	
Dry-off date	Limit date set by the farmer to dry-off all ewes of the flock that are still milking	–	Date		08/15/(n + 1)	
Selected free mating duration	Period set by the farmer during which rams can mate freely with ewes	–	Integer[3]	days	60	
Selected culling age	Age after which a ewe is considered by the farmer for culling	–	Integer	years	5	
Theoretical litter size	–	Tls	Integer	–	1	
Probability for the ewe to expect a twin litter	–	P_{TL}	Float	%	40	
Age of ram	–	–	Integer	years	3	
Suckling length	From lambing to weaning. Period of time where the ewes suckle the newborns	SL	Integer	days	28	*Database from a previous research project (*IDELE, 2014*)*
Selected turnover rate	Percentage of ewes to be renewed each year to keep a constant flock population	–	Float	%	28	

[1] Oestrus = period during which a female will allow mating; 2: Float = values that have potential decimal places; 3: Integer = whole numbers.

language (UML) class diagram.

Temporal scale: For the development of the REPROsheep model, the time step chosen was half a day (i.e., 12 h). The model simulated a breeding period followed by its milk production period, which corresponds to approximately 16 months (i.e., a total of 972 time steps in the model).

2.1.4. Process scheduling

A simulation started with the introduction of the rams for the ME in the spring of year 'n' and ended the day after the last day of the milking period in the summer of year 'n + 1'. The main processes represented in the model therefore took place during this period, called the 'production campaign', and the different agents represented could be involved in one or more of these processes (Table 2).

2.1.5. Design concepts

The model is considered dynamic and stochastic. Indeed, several processes responding to probability laws ruled the modelled reproduction mechanism: cyclicity and response to the male effect of the ewes (Section 2.1.7.SM2). Mating, abortion, lambing without any complications, having a twin litter and being in seasonal anoestrus at time t are events that were also estimated using probabilities set at the beginning of the simulation (Table 1a and 1b) and based on accumulated expert knowledge and technical criteria from previous projects.

Table 1b
Attributes and state variables of the REPROsheep model.

Attributes and state variables	Definition	Notation	Type	Units	Initial value/ range of values in the model	Source
Initial daily milk yield (for ewes > 1 year old)[1]	Daily milk production of an adult ewe on first day of milking after the suckling period	$IDMY_e$	Float	L	1–5	*Experimental data of* Debus et al. (2021)
Initial daily milk yield (for ewe-lambs < 1 year old)[2]	Daily milk production of a young ewe (<1 year) on first day of milking after the suckling period	$IDMY_{el}$	Float	L	1–5	*Database from a previous research project (*IDELE, 2014*)*
Third daily milk yield monitoring (of previous lactation)	Third milk yield monitoring, made on 4/11/n (during ewe's previous lactation). Usually, there is monitoring of an ewe's milk yield every 1 to 2 months during the milking period of the flock	TDMY	Float	mL	0–1640	*Experimental data of* Debus et al. (2021)
Last total milk yield	Total milk yield produced during the last lactation of the ewe	LTMY	Float	L	0–390	
Age of the ewe	–	Age	Integer	years	0–7	
Pre-mating body condition score	Score of 0 to 5, based on the level of muscling and fat deposition around the ewe's loin region (Russel et al., 1969). Here, the score is assessed one week prior to ram introduction for male effect.	BCS	Float	–	1.75–3.5	
Lactation number	Number of lactations performed by the ewe since the beginning of its productive life	$Lact_{num}$	Integer	–	1–8	
Lambing to male effect interval	Days between last lambing date and the date of rams introduction for male effect	LMEI	Integer	days	0–211	
Pregnancy length	–	PL	Integer	days	145–155	
Anoestrus	Ewe is at sexual rest and no oestrus behaviour (mating acceptance or heats) is observed	–	Boolean[3]	–	True	–
Cyclic before male effect	Ewe in oestrus before rams arrivals into the flock	CBME	Boolean	–	False	–
Responding to male effect	Ewes that were not cyclic before male effect and started to enter oestrus thanks to the 15 days of male effect	RME	Boolean	–	False	–
Show first oestrus	First ewe's oestrus after an anoestrus period	–	Boolean	–	False	–
In oestrus	–	–	Boolean	–	False	–
Pregnant	–	–	Boolean	–	False	–
Abortion	–	–	Boolean	–	False	–
Lambing	–	–	Boolean	–	False	–
Lactating	–	–	Boolean	–	False	–
Mating	–	–	Boolean	–	False	–

[1] Set randomly by a normal distribution, bound between 1 and 5, whose mean = 2.5 and standard deviation = 0.9 (from corresponding source).
[2] Set randomly by a normal distribution, bound between 1 and 5, whose mean = 1.9 and standard deviation = 0.9 (from corresponding source); 3: Boolean = can only be equal to yes or no.

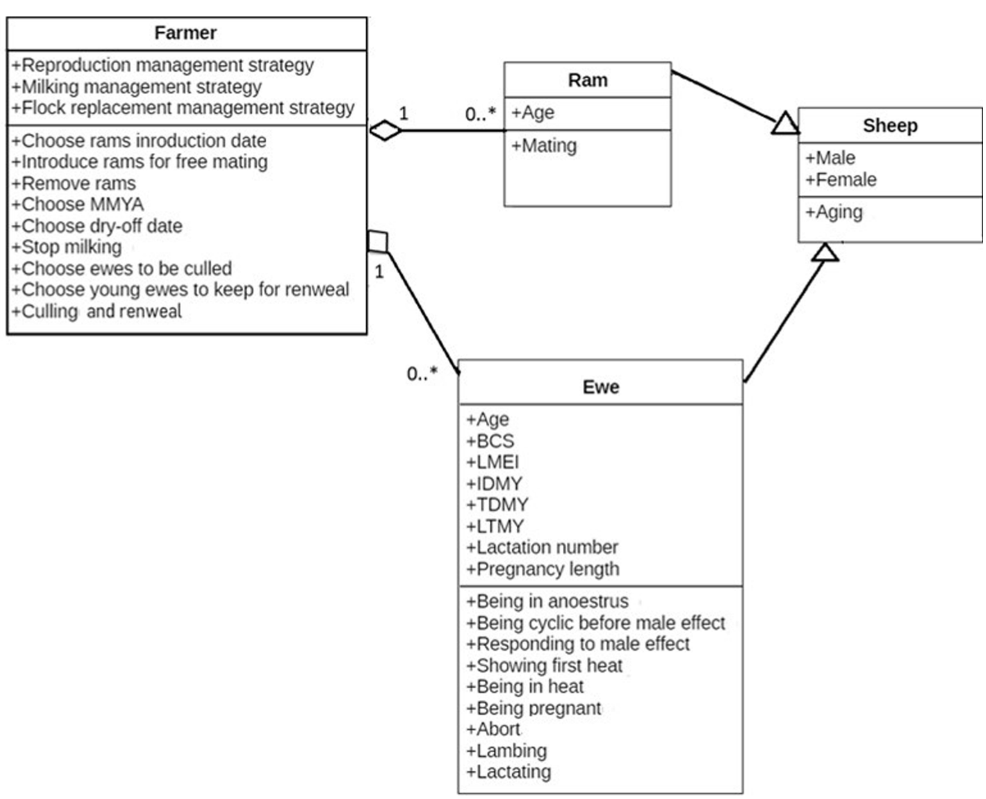

Fig. 2. Class diagram of entities in the REPROsheep model. Each block represents the model entities. The first portion of each block is the entity name, the second portion contains entity attributes and the third portion contains entities' principal actions.

Table 2
Main processes considered in the REPROsheep model.

Process	Agents implicated	Corresponding period	Sub-models
Reproduction management	Farmer	Mid-April (n) to mid-January (n + 1)	SM1
Reproduction activity	Ewes and Rams	Mid-April (n) to mid-January (n + 1)	SM2
Lactation	Ewes	October (n) to August (n + 1)	SM3
Milking management	Farmer	October (n) to August (n + 1)	SM4
Flock replacement management	Farmer	March (n + 1)	SM5

2.1.6. Initialisation

All simulations were initialised from the databases available in the literature and from the characteristics of the experimental flock monitored by Debus et al. (2021). To complete a full production campaign, each simulation started arbitrarily on April 17 of year 'n' (date of the ME) and ended on August 16 of year 'n + 1' (day after the end of milking arbitrarily set at August 15 of year 'n + 1'). The flock was initially composed of 51 Lacaune ewe lambs and 256 Lacaune ewes (i.e., 307 breeding reproductive females), for each of which we have pre-mating BCS, age, $Lact_{num}$, LMEI, TDMY and LTMY values for the year 'n'. (Table 1). The established ram:ewe ratio was 1 ram per 25 ewes (i.e., 12 rams in our case) so that the number of rams was sufficient for achieving the expected effective mating. The other main attributes and parameters of the model were fixed, and their initial values are provided in Tables 1a and 1b.

2.1.7. Submodels

The following paragraphs describe the different processes and actions represented in the model, as well as the modalities of the agents' action for each step:

Reproduction management: SM1

The main reproduction management actions or decision making executed by the farmer were as follows:

- *Choosing the date of ram introduction to achieve the ME:* The date of introduction of the rams for the ME was set arbitrarily by the farmer during the spring as it is commonly admitted in the Roquefort region that the Lacaune breed is not a strongly seasonal breed and therefore responds quite well to a ME in the spring. Once the rams were introduced in the flock, the male effect was considered to start on that date.
  All ewes were put to the ram as the modelled flock corresponds to a classic flock of the Roquefort basin area managed in such a way that the BCS pre-mating is acceptable for mating (i.e., BCS > 1.5; see range of values in Table 1b).
- *Introducing rams for free mating:* For adult ewes, the date of introduction of the rams for free mating was set by the farmer, each year, to be 15 days after the ME. For ewe lambs, by contrast, the date was arbitrarily chosen by the farmer to be close to the beginning of the natural sexual season (mid-summer). When this date was reached, the rams became active for mating.
- *Removing the free mating rams:* The duration of free mating was arbitrarily set by the farmer, and once ended, the rams were considered no longer active (without the possibility to mate with females).

Reproduction activity: SM2

The individual biological processes of reproduction correspond to a succession of transitions from one physiological stage to another over time. Such transitions are determined both by the technical management operations and decision making of the farmer (Fig. 1) and by other random events, including the particular individual features of the ewes. Debus et al. (2021) identified significant impacts of age, BCS pre-mating, milk yield observed in the previous lactation, and the last lambing date on the probability of being cyclic before the ME (i.e., in oestrus even before the rams are introduced) and on the quality of the response to the ME. These two events become critical during the off-season reproduction process when using the ME practice. Thus, they determined whether the transition from a seasonal anoestrus to an oestrus state, with oestrus appearance, should be expected (Fig. 3) and then followed by ovulations every 17 days (i.e., the length of a normal cycle in ewes) until fertilisation (Thimonier et al., 2000). Based on that, some probability equations were then considered for the events "Being cyclic before ME" (P_{CBME}) and "Responding to ME" (P_{RME}) (Table 3a). Ewe lambs started their mating season in mid-summer (close to the beginning of their natural breeding season) and started to be in oestrus spontaneously according to the probability of being in seasonal oestrus in mid-summer (Pso; Table 1a). Likewise, adult ewes that were not cyclic before ME and also did not respond to ME were mated again in mid-summer and subjected to Pso.

Once the ewe (ewe lamb or adult) was in oestrus, it was mated according to the farmer's strategy. Mated ewes were considered to be in the pregnancy stage based on the probability of success at mating (Pms). Once the pregnancy had started, a threshold of probability for abortion was considered (Pa), with two categories according to the timing of occurrence (i.e., early or late if the abortion occurs before or after the 45th day of pregnancy, respectively). In the 'early' cases, the ewe had the opportunity to return to oestrus, but if it was 'late', the ewe was not allowed to go back into oestrus and was separated from the breeding flock. At the end of pregnancy, without an abortion event, a probability to do an easy lambing (Pel), determined if the ewe was going to give birth or not. If the ewe was set to give birth normally, single or multiple litters were lambed, depending on the probability of lambing twins (P_{TL}). If the ewe turned out to have a difficult lambing, it was considered dead and no lambing took place.

Lactation: SM3

Lambing was followed by a 28-day suckling period (SL). At the end of this suckling period, lambs were weaned, and the ewe started to be milked. Individual milk yield during milking was calculated from an equation developed by Lagriffoul et al. (2003) for the Lacaune breed (Table 3b). This equation took into account the individual daily milk yield at the start of milking (IDMY) and the number of milking days, which was the difference in the number of days between the dry-off date and the start of milking date. IDMY values for each individual were randomly set using a normal distribution bound between 1 and 5 (i.e., the classic range of values for the milk production of a ewe in one day), whose mean and standard deviation were taken from previous research projects (Table 1b) and differed for adult ewes and ewe lambs. These mean and standard deviation values were considered to include differences in daily milk yield due to litter size and age.

Once started, milking ended either when the minimum acceptable daily milk yield set by the farmer was reached or upon the date defined by the farmer to end milk delivery (MMYA).

Milking management: SM4

A date for the end of milking was defined by the farmer. On this date, even if some ewes had not yet reached the minimum accepted production (MMYA), milking was stopped automatically, and the ewes were dried off.

Flock replacement management: SM5

For flock replacement, the main management decisions made by the farmer were as follows:

- *Culling ewes:* Once a year (on March 1st in this model), the farmer set a replacement rate and calculated the number of ewes to be culled, looking for a balance between the number of newborns and departures (so that the size of the flock remained more or less constant).

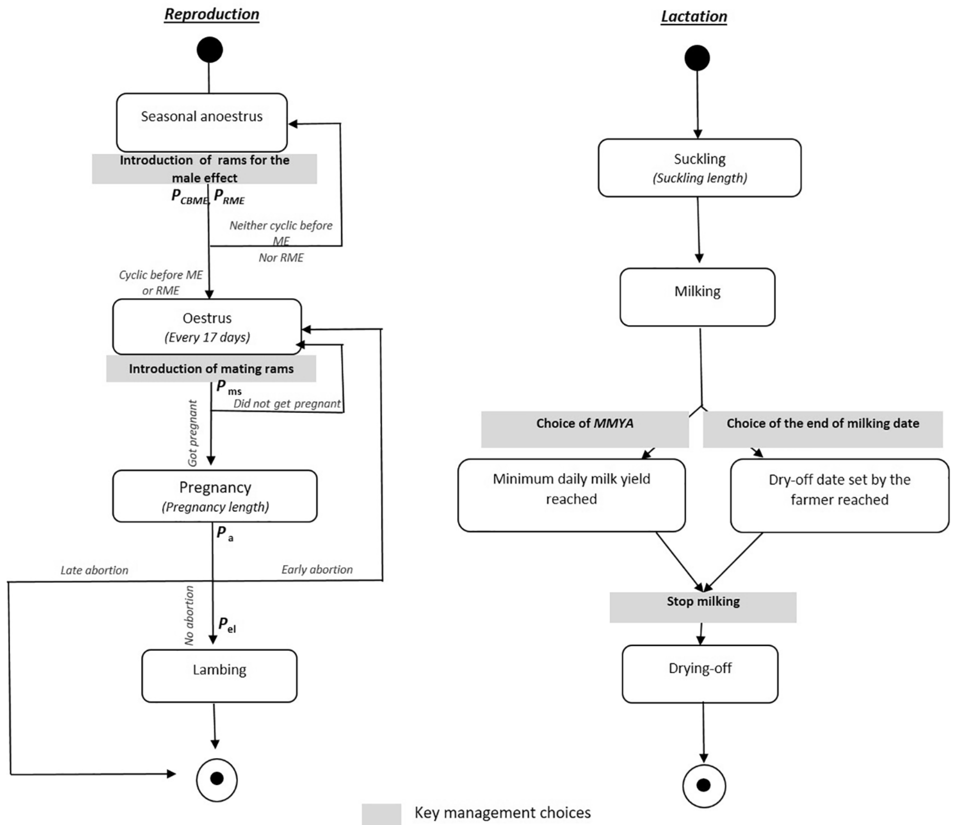

Fig. 3. The individual ewe reproduction and lactation phases were determined according to the sequence of physiological and/or biotechnical steps, including farmer decision making. Reproduction starts with an ewe in seasonal anoestrus and ends at lambing. Lactation starts just after lambing and ends with dry-off and includes subsequent phases, suckling (from lambing to weaning, for lamb rearing) and milking (from weaning to dry-off, for milk production purposes, without lamb presence).

Table 3a
Equations used for modelling individual reproductive processes.

Predictive equations[1]
Cyclicity before male effect (CBME):
$P_{CBME/BCS\leqslant 2} = exp(0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732)/(1 + exp(0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732))$
$P_{CBME/BCS\in]2-3]} = exp(0.592 + 0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732)/(1 + exp(0.592 + 0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732))$
$P_{CBME/BCS>3} = exp(1.212 + 0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732)/(1 + exp(1.212 + 0.103*Age + 0.008*LMEI + 0.007*LTMY - 0.002*TDMY - 2.732))$
Response to male effect (REM):
$P_{RME/BCS\leqslant 2} = exp(0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964)/(1 + exp(0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964))$
$P_{RME/BCS\in]2-3]} = exp(1.745 + 0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964)/(1 + exp(1.745 + 0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964))$
$P_{RME/BCS>3} = exp(2.871 + 0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964)/(1 + exp(2.871 + 0.276*Age + 0.011*LTMY - 0.002*TDMY - 1.964))$

[1] These logistic regression equations were developed from the experimental data set of Debus et al. (2021) to formalise the link between being cyclic before the male effect and the age, LTMY, TDMY and LMEI of each ewe and the link between responding to the male effect and the age, LTMY and TDMY of each ewe. BCS = pre-mating body condition score; LTMY = Last total milk yield; TDMY = Third daily milk yield; LMEI = Lambing to male effect interval; PCBME/BCS: Probability for an ewe to be cyclic before the male effect, as a function of its pre-mating BCS; PRME/BCS: Probability for an ewe to respond to the male effect, as a function of its pre-mating BCS.

Table 3b
Equations used for modelling individual lactation process.

Equations for calculating individual daily milk yield (L/day)[1]**:**
If ewe ($Lact_{num}\geqslant 1$) :
$Daily\ milk\ yield = IDMYe*exp(-[0.0028 + 0.0049*ln(IDMYe)]\ *\ Number\ of\ milking\ days$
If ewe lamb ($Lact_{num}\leqslant 1$) :
$Daily\ milk\ yield = IDMYel*exp(-[0.0021 + 0.0052*ln(IDMYel)]\ *\ Number\ of\ milking\ days$

IDMY = Initial daily milk yield.
[1] The coefficients of these daily milk yield equations come from the work of Lagriffoul et al. (2003).

Thus, the number of ewes culled was equal to the number of ewes × yearly replacement rate.
The ewes to be culled were chosen based on age (i.e., the oldest above the culling age set by the farmer) and those presenting difficulties at lambing. Old ewes to be culled were set to die on the day after the end of milking day and ewes presenting difficulties at lambing died at their lambing time.

- *Choosing ewe lambs for replacement:* At the same time, once a year (March 1st in this model), the farmer selected from all newborn females (<one year old) a percentage to be used to replace the culled ewes. The number of newborns to be retained to join the main flock was equal to the number of culled ewes.
- *Selling ewe lambs:* Once a year (on March 2nd in this model), ewe lambs that had not been chosen for replacement were sold.

For modelling purposes, farmer management practices have been deliberately simplified, and ewe lambs for replacement were selected randomly, considering that only one breeding campaign was simulated. However, it must be noted that in practice, there are other selection criteria, such as genetic index, health status or date of birth, that determine the number of ewes to be culled or retained.

2.2. Model outputs

At the end of each simulation, two dynamic outputs were observed: the distribution of the number of ewes lambing per week and the milk yield per week (in number of litres produced by all ewes at milking), as well as two punctual outputs: the total number of ewes lambing and the total milk yield of the flock, at the end of the campaign.

2.3. Stochasticity and choice of the number of repetitions for model analysis

As the REPROsheep model incorporated several stochastic processes, it was necessary to perform several replications for a given simulation. To determine the number of repetitions required for model validation and sensitivity analysis, an independent experiment was performed. The aim was to analyse the impact of the randomness of the simulations on the model outputs and find a threshold value of repetitions beyond which an increase in the number of repetitions would not imply a significant marginal decrease in the difference between the outputs. This exploration was carried out on the initial model described above (Section 2.1). Thus, the weekly number of ewes lambing, the weekly milk yield of the flock, the total number of ewes lambing and the total milk yield of the flock between the repetitions of a given simulation were compared. 150 replications of this simulation were performed and the variability between the outputs for 25, 50, 75, 100, 125 and 150 replications were compared.

Fig. 4, presents the median value by number of replicates over time for the outputs: weekly number of ewes lambing and weekly milk production of the flock. The results suggested that the increase in the number of repetitions beyond 25 did not have a significant impact on the overall trend of the weekly number of ewes lambing and weekly milk yield of the flock. Fig. 5A shows the box plots by number of repetitions of our two punctual outputs: total number of ewes lambing and total milk yield of the flock. From 75 repetitions, the median value of the total number of ewes lambing stabilised at approximately 267 ewes, and the median value of the total milk yield of the flock stabilised at approximately 60,500 L. It also appeared that beyond 75 repetitions, there were more "extreme" values, especially for total milk yield. Indeed, at 100 and 150 replicates, two total milk yield values were observed below 56,000 L. Moreover, Fig. 5B shows that from 75 repetitions, the standard deviation (sd) and thus the variance between the results of the repetitions for these two outputs seemed to be stable.

It was therefore decided to set the number of simulation repetitions required at 75 to minimise the calculation time required while trying to maintain realistic statistical properties, especially the appearance of extreme results.

2.4. Model validation

The model was validated using data from two commercial farms of

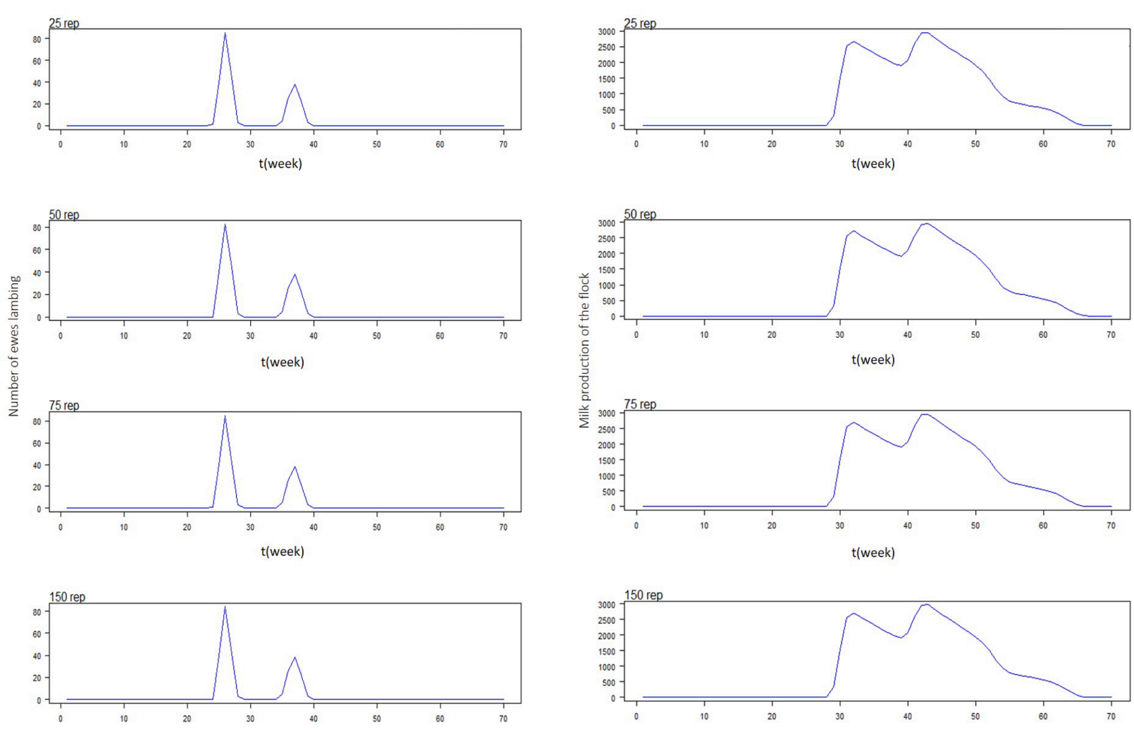

Fig. 4. Median of the number of ewes lambing and the milk production of the flock, per week, for 25, 50, 75 and 150 different repetitions.

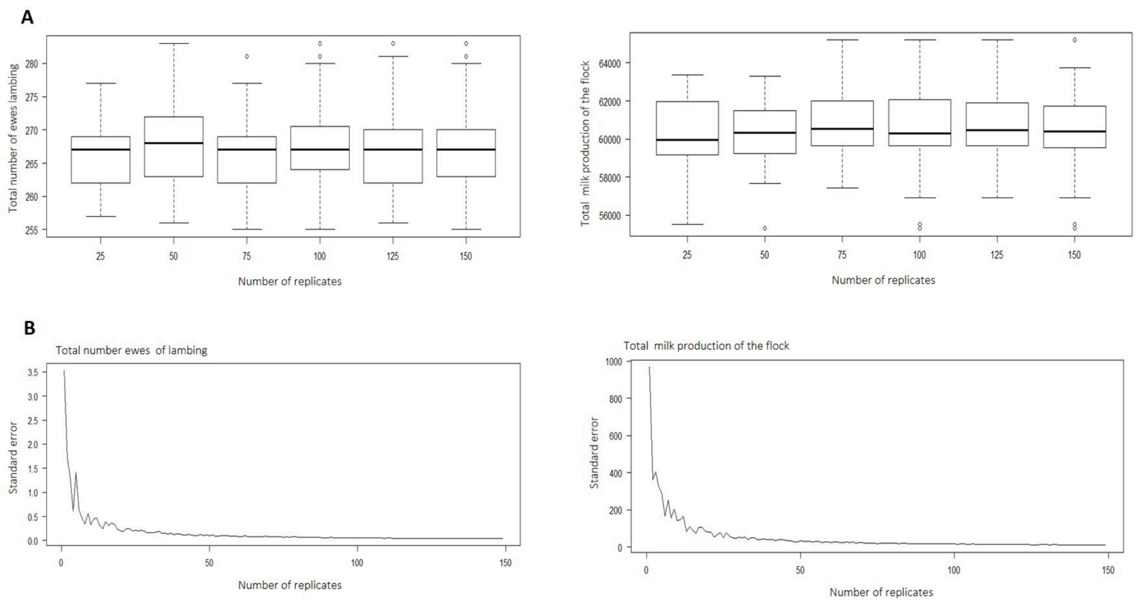

Fig. 5. (A) Box plot of the total number of ewes lambing and the total milk production of the flock per number of repetitions. (B) Standard error of the total number of ewes lambing and the total milk production of the flock per number of repetitions.

the Roquefort area. These data were extracted from the SIOEL database, which is an information system implemented for dairy sheep in France, to manage genetic and techno-economic data (Astruc et al., 2008). Both commercial farms managed reproduction without hormones, with a first mating in April (i.e., off-season). Adjustments to the model parameters were made to match the flock management specificities of each farm. Each simulation was repeated 75 times to take into account the model stochasticity (Section 2.3). The total number of ewes lambing and the total milk yield of the commercial farms were then compared with the simulated ones by calculating prediction errors. The correlations between the mean values of dynamic simulated outputs (weekly number of ewes lambing and monthly milk yield) and the same observed performances in the commercial farms were also calculated.

2.5. Sensitivity analysis

A sensitivity analysis was performed to identify the parameters that most contributed to the variability of the outputs. This analysis, similar to the one performed by Lurette et al. (2009), followed the methodology developed by Lamboni et al. (2009) that allows to analyse time series outputs by combining principal component analysis and analysis of variance. Sensitivity indices were then proposed to synthesise the influence of each parameter on the whole time series output.

All analyses were performed using R 3.6.2 software (R Core Team, 2019). The Multisensi package (Bidot et al., 2018) was used to analyse the dynamic outputs, and ANOVA was performed on the mentioned punctual outputs.

2.5.1. Experimental design for sensitivity analysis

The model presented 12 input parameters and variables that could influence the output results. To study the sensitivity of the simulation outputs to these different parameters and variables, a factorial design, in which each of the input parameters (called factors) had two levels of extreme values, was built (Table 4). For each factor, the range of values chosen was set arbitrarily between a low and a high value, regardless of what can be observed in the field, the aim being to analyse the sensitivity of the simulation tool to its input parameters.

A complete factorial design for 12 factors at 2 levels each corresponds to $2^{12} = 4096$ possible combinations of these factors. To reduce the number of combinations to be studied, a fractional factorial design of resolution IV using the FrFr2 function of R software (Grömping, 2014) was carried out. This IV resolution made it possible to estimate the main effects and the two-by-two interactions of factors, assuming that the higher-order interactions were negligible. Thus, a fractional factorial design composed of 32 combinations of our study factors was established. Seventy-five repetitions of each were needed to take into account the stochasticity of the model. Therefore, our sensitivity analysis was performed on the results of $32 \times 75 = 2400$ simulations.

Table 4
Input parameters and values for the model sensitivity analysis.

Input parameters and variables	Unit	Level	
		Low value	High value
BCS (mean)	–	1.5	3.5
Age (mean)	–	2	4
TDMY (mean)	ml	500	1000
IDMYe (mean)	L	2.3	2.8
IDMYel (mean)	L	1.7	2.2
LTMY (mean)	L	100.0	300.0
LMEI (mean)	days	90	180
Pa	%	1	3
Pel	%	92	100
Pms	%	40	60
Pso	%	70	90
MMYA	L	0.6	1.0

BCS = pre-mating body condition score; IDMYe = Initial daily milk yield (for ewes > 1 year old); IDMYel = Initial daily milk yield (for ewe-lambs < 1 year old); LTMY = Last total milk yield; LMEI = Lambing to male effect interval; MMYA = Minimum milk yield accepted at milking; TDMY = Third daily milk yield; Pel = Probability of an easy lambing; Pso = Probability to be in seasonal oestrus; Pa = Probability of abortion; Pms = Probability for a successful lambing

2.5.2. Analysis of punctual outputs

Two ANOVAs were performed on the results of the 2400 simulations to compare the influence of the 12 factors on each punctual output (total number of ewes lambing and total milk yield of the flock). A factor was considered significant when the p-value <5%. Then the contribution of the factors to the variability of each output was quantified by calculating the ratio between the sum of squares of each significant factor (including interactions) and the total sum of squares for all of the factors studied.

2.5.3. Analysis of dynamic outputs

Following the method proposed by Lamboni et al. (2009), it was first considered that dynamic outputs can be represented as tables built of N rows and p columns, where $N = 2400$ (number of simulations) and $p = 70$ (number of successive time points, i.e., the number of weeks during which the dynamic output was observed). A principal component analysis (PCA) with N individuals and p variables was then performed to provide linear combinations (also called components) of the initial p variables explaining the maximum inertia (i.e., variability) between the simulation outputs. Only the first three principal components (PCs) were retained, as they were sufficient to cover most of the variability observed between simulations. The PCA provided a score on each component for each simulation (i.e., for each row on tables). A final step consisted of an ANOVA, including the main and the two-factor interaction effects on the simulation scores, for each of the components considered. Sensitivity indices (SI), corresponding to the main effect or interactions, were then calculated for each factor and for each component. An effect was considered significant when SI > 5%.

2.6. Virtual experiment: Impact of flock composition

Once the validity and sensitivity of the model were studied, different flock composition scenarios were tested using the simulator. The impact of the flock distribution of ages (Age), pre-mating BCS and total milk yields from previous lactation (LTMY), which are the three main factors that impact the probabilities of being cyclical off-season and responding to the male effect (Debus et al., 2021), was studied. These are also factors that can vary greatly from one farm to another, with potential farmer intervention to modify them. To study the impact of these three parameters and their distribution on model outputs, a virtual experiment including the analysis of five flock management scenarios was carried out. To take into account the stochasticity of the model, each scenario was simulated 75 times. Table 5 presents the tested scenarios. The reference scenario (*Ref*) corresponds to the composition of the flock during one of the years of the Debus et al. (2021) monitoring study. Since BCS is an intrinsic trait of the ewe that the farmer can influence (e.g., by adapting feeding strategy), the effect of a variation in the flock's distribution with regard to the ewes' pre-mating BCS, compared to the reference scenario (i.e., *BCS−* and *BCS+* scenarios), was first studied. Then, two extreme theoretical scenarios, for which the three parameters pre-mating BCS, Age and LTMY evolve in the same way and at the same time (*All−* and *All+* scenarios), were studied. It was decided to test scenarios where the mean values of these parameters distributions only evolve by 0.5 units (for age and BCS) or 50 L (for milk yield); these evolutions being considered as theoretically plausible by the experts of the French dairy sheep production, assuming some efforts on feed management in particular.

For each scenario that differs from the reference scenario, the individual values of BCS for all ewes and LTMY of adult ewes (i.e., that have already produced milk before) were obtained by randomly sampling a normal distribution whose mean was set according to the scenario (Table 5) and standard deviation was equal to the reference scenario's. For ewe lambs, LTMY was specifically set to zero. The age of each ewe was obtained by randomly sampling a Poisson distribution whose mean was set according to the scenario (Table 5).

As the focus was only on the impact of individual ewe characteristics on the number of ewes lambing and milk yield of the flock, the management of reproduction by the farmer and the size of the flock were the same for all five scenarios.

Table 5
Description of the flock scenarios.

Scenario	Description	BCS		Age (Years)		LTMY* (L)	
		Mean	sd	Mean	sd	Mean	sd
Ref	*Ref*erence scenario	2.5	0.3	2.5	1.9	195	65.8
BCS−	Mean BCS lower than *Ref* scenario's	2	0.3	2.5	1.9	195	65.8
BCS+	Mean BCS higher than *Ref* scenario's	3	0.3	2.5	1.9	195	65.8
All−	Mean BCS, mean Age and mean LTMY lower than *Ref* scenario's	2	0.3	2	1.9	145	65.8
All+	Mean BCS, mean Age and mean LTMY higher than *Ref* scenario's	3	0.3	3	1.9	245	65.8

BCS = pre-mating body condition score; LTMY = Last total milk yield; sd = standard deviation

* Mean and sd of LTMY values distribution for adult ewes only (i.e., ewes that have already produced milk before).

2.7. Statistical analyses of scenario results

Scenario results were expressed as the means of simulation repetitions.

2.7.1. Total number of ewes lambing and total milk yield of the flock

Two one-factor ANOVAs were performed to study (i) the scenario effect on the total number of ewes lambing and (ii) on the total milk yield of the flock. The lambing rate (total number of ewes lambing in relation to the number of females put to reproduction) for each scenario was also calculated for the modelled campaign.

2.7.2. Number of ewes lambing per week

The modelled management strategy induced two periods of lambing corresponding to lambing from a spring breeding campaign with synchronisation of oestrus using ME and to lambing from seasonal breeding (including lambing of ewe lambs). To simplify the study of the scenarios, two lambing periods over the entire reproduction campaign were defined, and the weekly number of ewes lambing in each period was added to compare simulation results for each of these two periods. The first lambing period, named P1, corresponding to the days between the 24th and 28th weeks of simulation (i.e., between September 25th and October 23th) of year 'n'. The second lambing period, named P2, corresponding to the days between the 35th and 39th weeks of simulation (i.e., between December 11th of year 'n' and January 8th of year 'n + 1').

A one-factor ANOVA was then carried out for each period to evaluate the scenario effects on the number of ewes lambing over a given period (P1 or P2). The proportion of the total number of ewes lambing (in %) over each period (P1 and P2) was also calculated.

2.7.3. Weekly milk yield of the flock

Individual daily milk yield was modelled by a decreasing exponential function (Lagriffoul et al., 2003), with the highest values obtained at the beginning of lactation. The modelled management strategy therefore assumed two milk yield peaks for the flock: a first one linked to the individual milk yield of ewes that lambed during period P1 and a second one linked to those ewes that lambed during P2. A single-factor ANOVA was thus performed for each flock milk yield peak to evaluate the scenario effects on the flock milk yield at each of these peaks.

3. Results

3.1. Model validation

The model slightly underestimated the total number of ewes lambing as well as the total milk yield, for each of the two farms, with an average prediction error, across the two farms, of −5.5% for each of those two outputs. For the dynamic outputs (weekly number of ewes lambing and monthly milk yield), depending on the farm and on the week observed, the model either overestimated or underestimated the outputs values

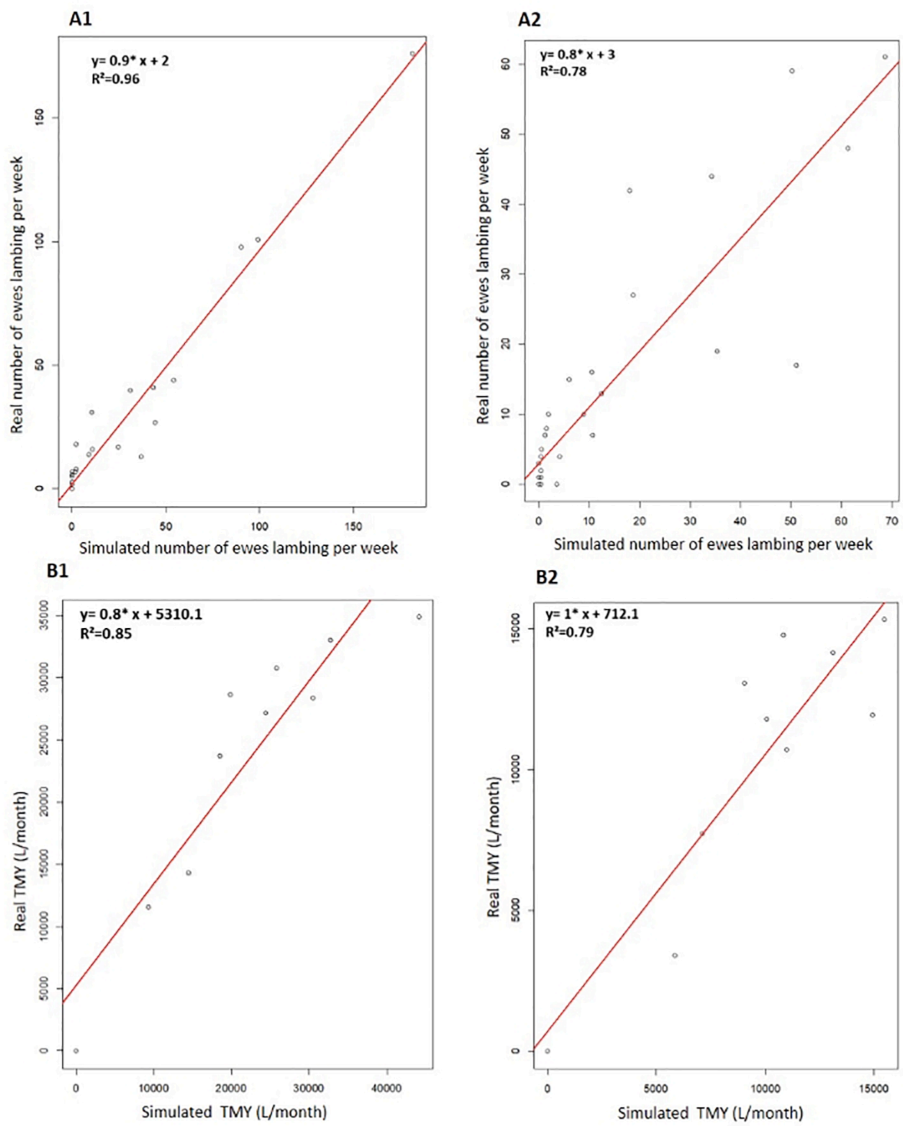

Fig. 6. Means (n = 75) of simulated (A) number of ewes lambing per week and (B) total milk yield (TMY) per month compared to observed values on each farm (1 and 2).

(Fig. 6). However, overall, high correlations, (from 0.78 to 0.96, Fig. 6) between the mean values of each dynamic simulated outputs and their corresponding observed values, were found for each of the two farms of the SIOEL database.

3.2. Sensitivity analyses

3.2.1. Influence of factors on the total number of ewes lambing and on the total milk yield for one production campaign

Table 6 presents the overall contributions of the 12 factors studied to the sensitivity of the outputs “total number of ewes lambing” and “total milk yield of the flock”.

The sensitivity of the output “total number of ewes lambing” was related, by more than half, to the Pel. The factors Pso and LTMY also contributed, together, to more than 25% of the overall sensitivity. The age of the ewes and their pre-mating BCS also had a small influence on the “total number of ewes lambing” output, with a contribution of less than 10%. For the output “total milk yield of the flock”, MMYA was the factor with the highest contribution, more than twice that of ewes’ IDMYe (23%).

3.2.2. Influence of factors on the number of ewes lambing per week

For the number of ewes lambing per week, 80.1% inertia was obtained for the first main component (PC1; Fig. 7A). This means that this component alone explained the most important part of the variability observed between the 2400 simulations for this output. Therefore, only the result of this first component was detailed here.

The factors that contributed most to the variability in the number of ewes lambing events over time (SI > 5%) were, in decreasing order, LTMY, age, pre-mating BCS and TDMY, with total sensitivity indices (TSIs) of 43.3%, 22.3%, 18.7%, and 11.6%, respectively (Fig. 7B). The variability of the output depended almost identically on the main effect of these four factors and on their two-way interactions.

3.2.3. Influence of factors on the weekly milk yield of the flock

For the output “weekly milk yield of the flock”, it was found that the first two main components (PC1 and PC2) had inertia values of 52.1% and 41.6%, respectively (Fig. 8A). Together, these two components had an inertia of 93.7% and explained most of the variability observed between the 2400 simulations for this output. Therefore, only the results of these two components was detailed below.

The most influential factors (SI > 5%) on the weekly flock milk yield

Table 6
Factor contributions to the sensitivity of the total number of ewes lambing and milk yield of the flock for one lactation.

Factors	Contribution to sensitivity (%)	
	Total number of ewes lambing	Total milk yield (L per flock)
BCS	5.72	0.97
Age	8.55	1.71
TDMY	2.66	0.79
LTMY	11.90	1.90
LMEI	0.06	0.24
Pel	55.48	8.97
Pso	14.50	2.41
Pa	1.07	0.18
Pms	0.02	ns
MMYA	0.03	60.08
IDMYe	ns	22.72
IDMYel	ns	0.01

ns = non-significant at p-value < 0.05; BCS = pre-mating body condition score; IDMYe = Initial daily milk yield (for ewes > 1 year old); IDMYel = Initial daily milk yield (for ewe-lambs < 1 year old); LTMY = Last total milk yield; LMEI = Lambing to male effect interval; MMYA = Minimum milk yield accepted at milking; TDMY = Third daily milk yield; Pel = Probability of an easy lambing; Pso = Probability to be in seasonal oestrus; Pa = Probability of abortion, Pms = Probability for a successful lambing.

for PC1 were LTMY, MMYA, Age, BCS and TDMY at their last lactation. Their two-way interactions contributed almost identically to the variability of this output.

The second main component (PC2) revealed the factors that reduced the difference between the two peaks of milk yield while at the same time revealing the presence of a small peak at the end of the milking period. PC2 essentially presented the effects of the MMYA (TSI = 52.6%) and IDMYe (TSI = 21.3%) factors (Fig. 8B).

3.3. Virtual experimentation (scenarios)

3.3.1. Total number of ewes lambing and total milk yield of the flock at the end of the production campaign, according to the scenarios

For the total number of ewes lambing as well as for the total milk yield of the flock, a significant effect ($p < 0.05$) of the simulated scenario was observed. Only the *BCS−* scenario did not differ from *Ref*. The number of ewes lambing for *BCS+* (277 ewes i.e., a 90% lambing rate) and *All+* (282 ewes, 92% lambing rate) were significantly higher than the number of ewes lambing obtained in *Ref* (273 ewes, 89% lambing rate) (Fig. 9A). On the other hand, the number of ewes lambing in *All−* (266 ewes, 87% lambing rate) was significantly lower than in *Ref* (Fig. 9A).

Similarly, for the total milk yield of the flock, a significant positive effect of the *BCS+* (+1172 L) and *All+* (+2309 L) scenarios, compared to *Ref,* was observed. In contrast, a significant negative effect of *All−* (−1214 L) was observed for this parameter. No significant effect was found with *BCS−* (Fig. 9B).

3.3.2. Number of ewes lambing per week according to the scenarios

The number of ewes lambing over time differed according to the scenarios (Fig. 10A). A significant effect ($p < 0.05$) of the scenarios on the average number of ewes lambing was observed for the two lambing periods P1 (weeks 24–28) and P2 (weeks 35–39). On both P1 and P2, the average number of ewes lambing in the *BCS+* (P1: 218; P2: 59), *All−* (P1: 162; P2: 103), and *All+* (P1: 243; P2: 39) scenarios were significantly different from *Ref* (P1: 200; P2: 72; Fig. 10B and 10C).

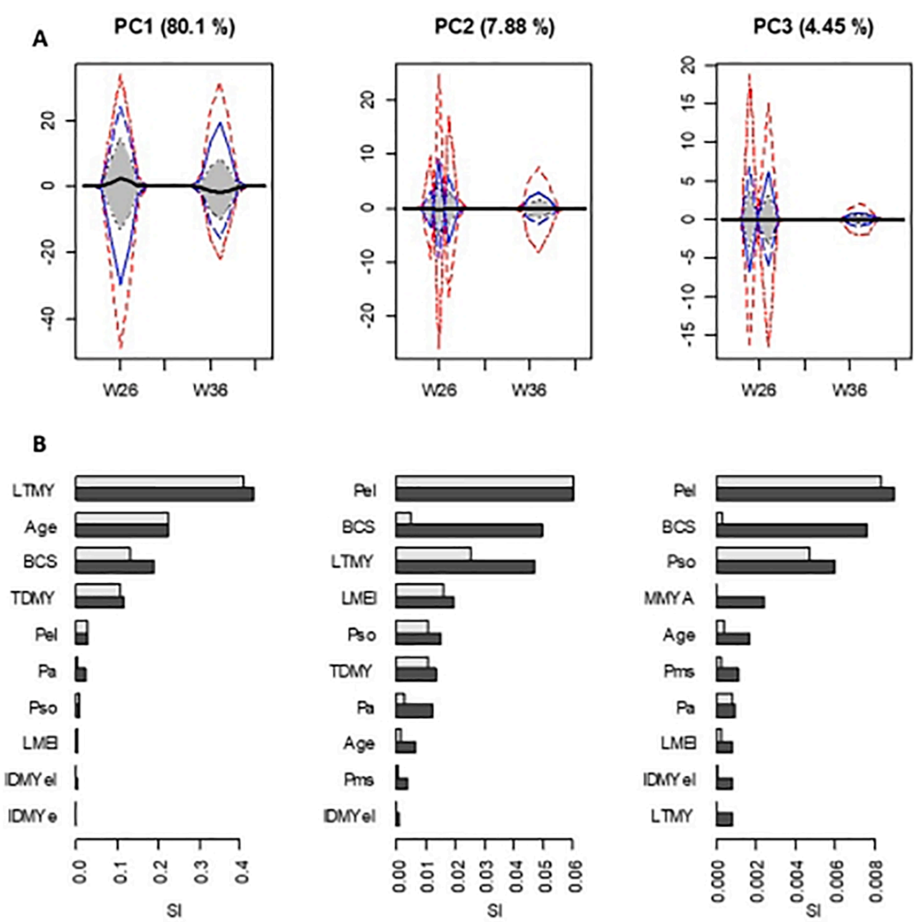

Fig. 7. Sensitivity analysis of the number of ewes lambing over time: results of ANOVA performed for the first three components (inertia: 80.1%, 7.9%, 4.5%). (A) Loadings defining the principal component for each time variable (in abscissa) and (B) total sensitivities for the 10 most influential factors ranked in descending order. Sensitivities are split into main effects (black) and two-way interactions (grey). BCS = pre-mating body condition score; IDMYe = Initial daily milk yield (for ewes >1 year old); IDMYel = Initial daily milk yield (for ewe-lambs <1 year old); LTMY = Last total milk yield; LMEI = Lambing to male effect interval; MMYA = Minimum milk yield accepted at milking; TDMY=Third daily milk yield; Pel = Probability of an easy lambing; Pso = Probability to be in seasonal oestrus; Pa = Probability of abortion; Pms = Probability for a successful lambing

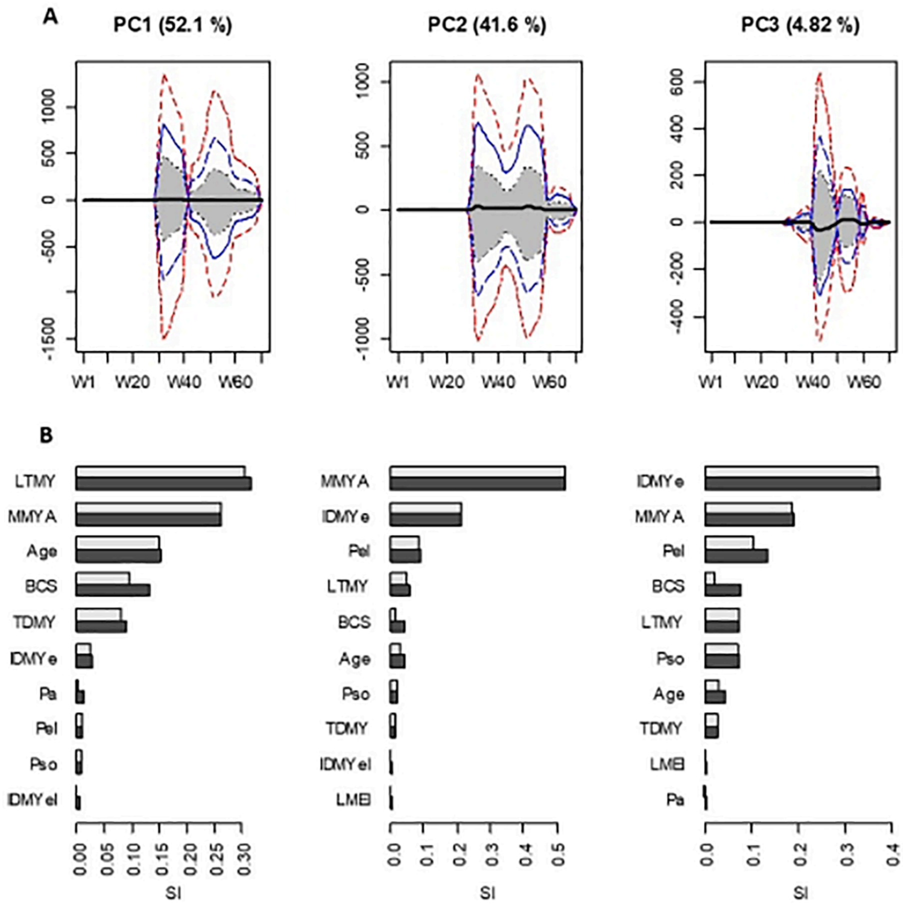

Fig. 8. Sensitivity analysis of flock milk production over time: results of ANOVA performed for the first three principal components (inertia: 52.1%, 41.6% and 4.8%). (A) Loadings defining the principal component for each time variable (in abscissa) and (B) total sensitivities for the 10 most influential factors ranked in descending order. Sensitivities are split into main effects (black) and two-way interactions (grey). BCS = pre-mating body condition score; IDMYe = Initial daily milk yield (for ewes >1 year old); IDMYel = Initial daily milk yield (for ewe-lambs <1 year old); LTMY = Last total milk yield; LMEI = Lambing to male effect interval; MMYA = Minimum milk yield accepted at milking; TDMY = Third daily milk yield; Pel = Probability of an easy lambing; Pso = Probability to be in seasonal oestrus; Pa=Probability of abortion; Pms = Probability for a successful lambing

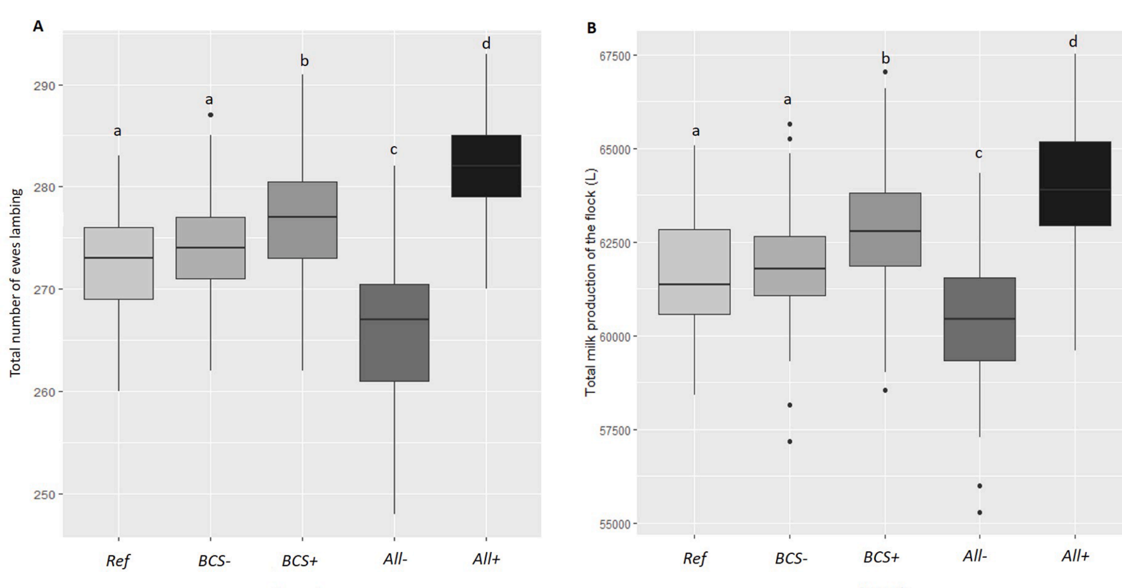

Fig. 9. (A) Boxplot of the number of ewes lambing; (B) Boxplot of the total milk production of the flock for a campaign full lactation period (n = 75 repetitions per scenario). Ref = Reference flock scenario; *BCS*−, *BCS*+, *All*−, *All*+ = Alternative scenarios to Ref. a,b,c,d: Values with a separate letter differ at p-value <0.05.

Over the P1 period, a higher number of ewes lambing was observed in *BCS*+ and *All*+ than in *Ref* (79% and 86% of the total number of ewes lambing achieved, compared to 73% in *Ref*, respectively). As a result, the number of ewes lambing over the P2 period was lower in *BCS*+ and *All*+ (21% and 14% of the total number of ewes lambing) than in *Ref* (27% of the total number of ewes lambing). The *All*− scenario led to a lower number of ewes lambing compared to *Ref* in P1 (61% of the total number of ewes lambing versus 73%, respectively), which resulted in a higher number of ewes lambing than *Ref* in P2 (39% of the total number of ewes lambing versus 27%, respectively, for *All*− and *Ref*).

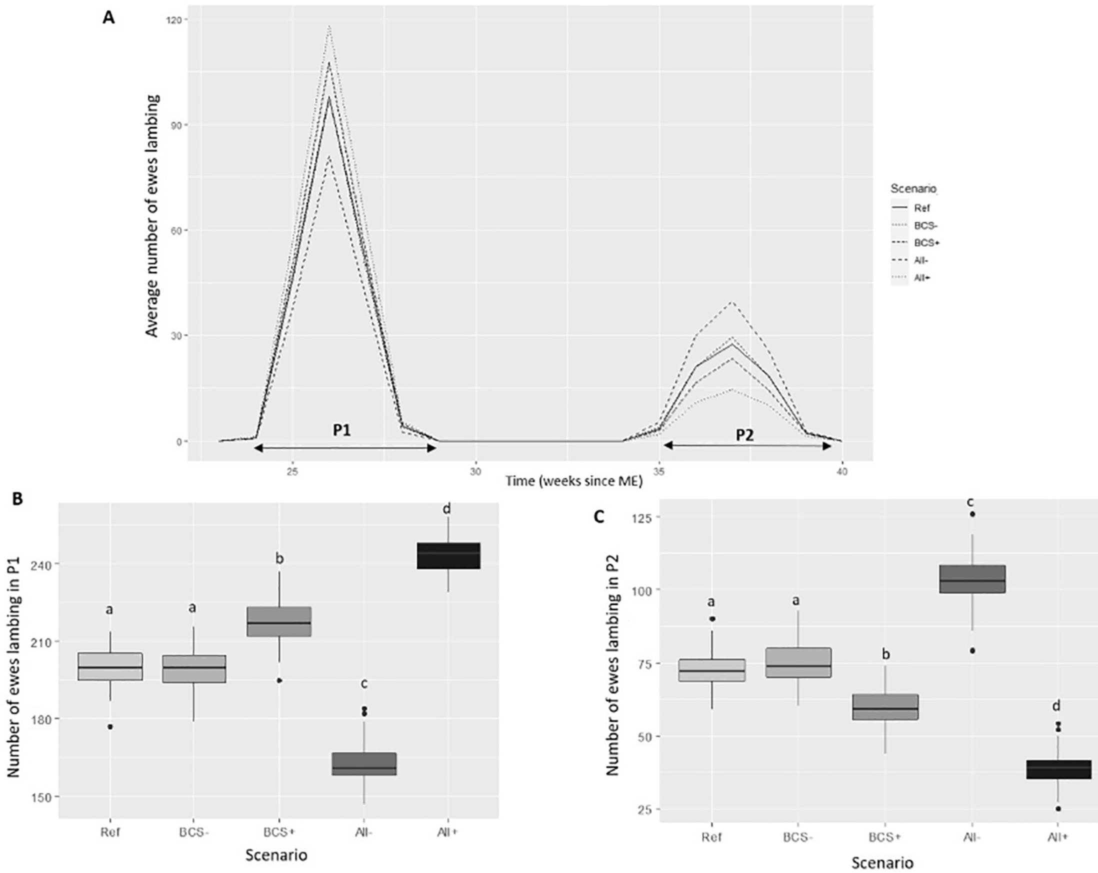

Fig. 10. (A) Average number of ewes lambing per week according to the flock scenarios (n = 75 repetitions per scenario) between the 24th and 39th weeks from the start of the simulation (in our case, the male effect date (ME)); P1 = first lambing period between weeks 24 and 28, P2 = second lambing period *(weeks 35–39). (B)* Boxplot of the number of ewes lambing during P1 for each scenario. (C) Boxplot of the number of ewes lambing during P2 for each scenario. Ref = Reference flock scenario; *BCS*−, *BCS*+, *All*−, *All*+ = Alternative scenarios to Ref. a, b, c, d: For each period, values with a separate letter differ at a p-value <0.05.

3.3.3. Weekly milk production of the flock according to the scenarios

Two peaks of milk production were seen (Fig. 11A): the first one at the 32nd week of simulation and the second at the 42nd week of simulation, i.e., 3 weeks after the end of each lambing period (P1 and P2). A significant effect ($p < 0.05$) of the scenarios on the overall flock milk yield at these 2 peaks was also observed.

For the first peak, the comparison of the scenarios highlighted a significant difference ($p < 0.05$) between *BCS*+, *All*−, *All*+ and *Ref* (Fig. 11B). Indeed, at the first peak of weekly milk yield, the ewe flock produced more in *BCS*+ and *All*+ than in *Ref* (+9% and + 22%, respectively, compared to *Ref* milk yield at peak 1). On the other hand, milk yield was lower in *All*− (−18%) than in *Ref*. At the second peak of weekly milk yield, only *All*− and *All*+ presented milk yields significantly different from *Ref* (Fig. 11C), which resulted in an additional 128 L of milk when adopting the *All*− scenario (i.e., +4% compared to *Ref)* and an average reduction of 84 L with *All*+ (i.e., −3% compared to *Ref)*.

4. Discussion

This dairy sheep flock, was built aiming to simulate the overall productive and reproductive performance of the flock based on the aggregation of individual ewe performance. Thanks to the dynamic modelling of the oestrus occurrence process, the model integrated a representation of the variability of individual responses to hormone-free reproductive management. Sensitivity analyses of the model have shown that age, pre-mating BCS and LTMY are factors that had an important impact on the simulated variability in lambing events number and distribution, as well as on the simulated milk yield of the flock over time (i.e., on the performances of the flock). Results obtained have also shown that the proposed model took into account particular relationships between individual ewe characteristics and their related individual reproductive performance. Indeed, several authors have reported a positive correlation between BCS and reproductive performance (Vatankhah et al., 2012; Kenyon et al., 2014). A positive effect of age on reproductive performance has also been demonstrated (Festa-Bianchet and King, 2007; Maatoug-Ouzini et al., 2013; Meraï et al., 2014). In contrast, the effect of milk yield on the reproductive performance of dairy ewes is still controversial. David et al. (2008) observed a negative genetic correlation between milk yield and fertility to animal insemination in Lacaune ewes, whereas Kassem et al. (1989) and Gootwine and Pollott (2000) found no significant effect of milk yield on the postpartum reproductive performance of ewes. Debus et al. (2021), whose experimental data were used to model the process of oestrus occurrence here, showed that there was a combined effect of age, pre-mating BCS and milk production level on the occurrence of ewe oestrus following ME.

The sensitivity of the outputs to individual input factors has also shown that this model effectively captured the relationship between the diversity of individual ewe features (age, pre-mating BCS and milk yield) and the overall flock performance. This is an original finding considering that it was not possible in previous existing sheep flock models, where reproductive success was previously fixed by deterministic decision rules or randomly chosen within a fixed range of values (Lesnoff, 1999; Gebre et al., 2014). Only a few sheep models integrated some individuality and randomness, mainly through the integration of fertility and fertilisation probabilities that depended, among other things, on indicators specific to each ewe (success or failure in the previous

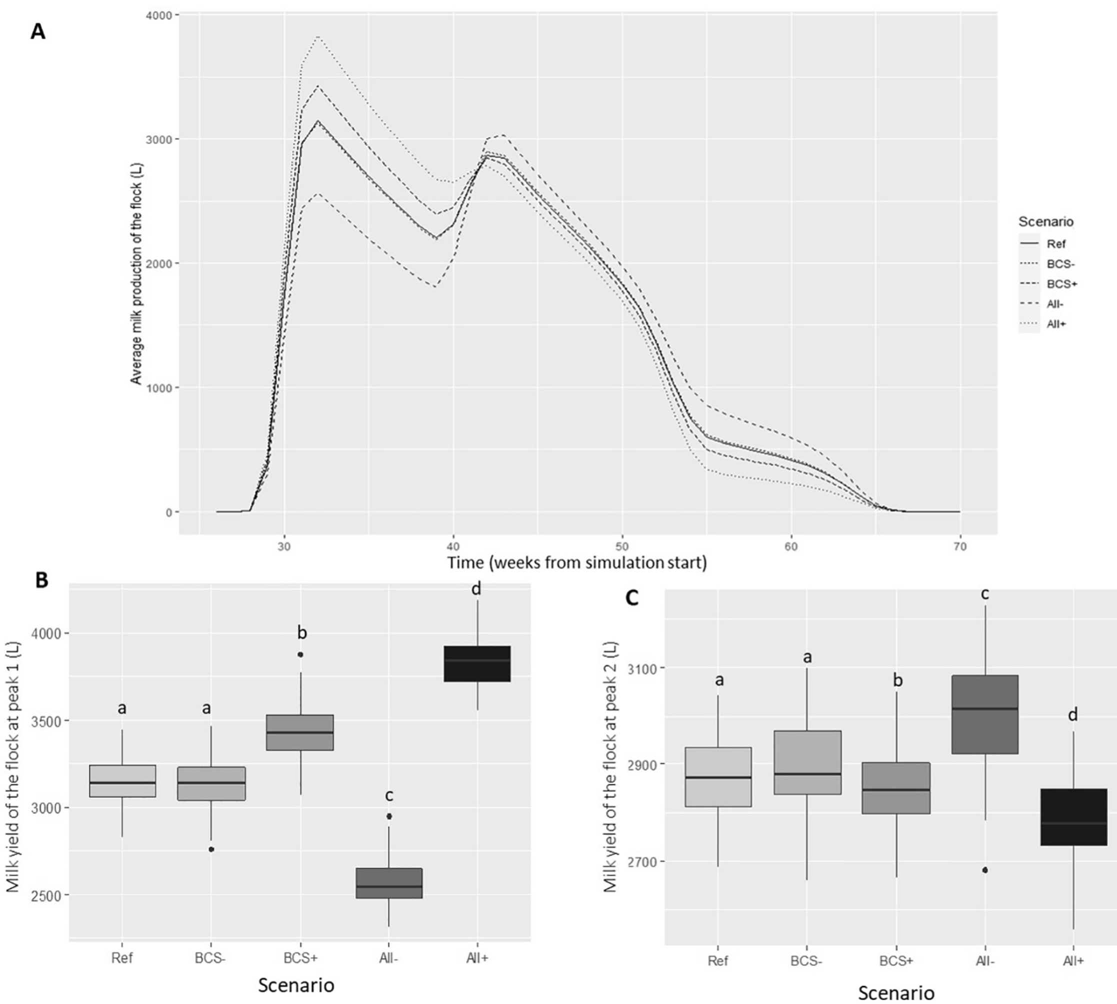

Fig. 11. (A) Flock's average weekly milk production, according to the flock scenarios (n = 75 repetitions per scenario). (B) Boxplot for flock milk production at peak 1 for each scenario. (C) Boxplot for flock milk production at peak 2 for each scenario. Ref = Reference flock scenario; *BCS−*, *BCS+*, *All−*, *All+* = Alternative scenarios to Ref. a, b, c, d: For each period, values with a separate letter differ at a p-value <0.05.

breeding season; Cournut and Dedieu, 2004), for example.

The model developed here also appears to be a good tool for exploring the link between flock structure, the related management strategies shaping it, and expected flock performance. This study could contribute to optimising the management of reproduction in sheep farming with hormone-free ambitions and goals. Indeed, the productive and reproductive performances of a flock are significantly affected by management practices, as illustrated by the high sensitivity of the flock's milk production to the MMYA set by the farmer in the model (SI < 60%). However, these parameters are also strongly conditioned by the different individual biological mechanisms operating for each individual (Puillet et al., 2010a). Several models aiming to study or optimise herd performances were thus designed to represent the variability of the biological response to various feed and/or reproduction management practices. The integration of this variability is generally made through the modelling of individual biological mechanisms, such as the partitioning of nutrients in the processes of milk production and constitution of body reserves (Puillet et al. (2008) in their dairy goat herd model; Cadéro et al. (2018) in their pig herd model; Villalba et al. (2019) in their dairy ewe model) or the oestrus and heat mechanism in the reproductive process (Oltenacu et al. (1980) and Brun-Lafleur et al. (2013) in their dairy cattle herd model). These different mechanisms are key elements to consider in livestock production and are the result of interactions with farmers' management strategies and decision making. They are driven, however, by specific individual characteristics of the animal, which add complexity to the whole picture (e.g., production potential, Puillet et al., (2008); BCS, Brun-Lafleur et al., (2013)).

The different flock scenarios simulated in this study allowed to explore the extent to which age, pre-mating BCS and milk yield level affect flock performance during a production campaign. Scenarios corresponding to a pre-mating BCS increase alone (*BCS+*) and a combined increase in pre-mating BCS, age and milk yield in the flock (*All+*) led to an improvement in productive and reproductive performance. Indeed, a gain of 1% (*BCS+*) and 3% (*All+*), respectively, on the rate of ewes lambing in the flock was observed, which correspond to 4 and 9 additional ewes lambing, respectively, compared to *Ref*. Similarly, a gain of 2% (*BCS+*) and 4% (*All+*), respectively, was observed on the flock's milk yield compared to *Ref*, which correspond to +1560€ and +3080€ in milk sales, respectively, in the current context where the price of French organic milk is 1334€/1000 L (DRAAF Occitanie, 2021). It would therefore appear that a pre-mating BCS increase, alone or in association with an increase in age and individual milk yield, would lead to an improvement in performance at the flock level. It can therefore be assumed that the demonstrated effects of age, pre-mating BCS and milk yield on individual performance have been reflected in the overall performance of the flock.

Scenarios corresponding to a single pre-mating BCS decrease (*BCS−*) and to a joint decrease in the pre-mating BCS, age and milk yield in the flock (*All−*) led to a decrease in the productive and reproductive performance of the flock. However, only the decrease caused by the *All−*

scenario was significant. The pre-mating BCS decrease alone (*BCS*−), contrary to what might have been expected, did not have a significant impact on flock performance (punctual and dynamic). This may be due to the fact that for the Lacaune breed, as for many other breeds, there is an optimal pre-mating BCS at which a significant effect on ewe performance is observed. Above and below this optimal value, lower reproductive performances are generally observed (Yilmaz et al., 2011, Vatankhah et al., 2012). The optimal value differs according to the breed. For the Manchega ewe, for example, Molina et al. (1994) identified an optimal pre-mating BCS of 3, whereas it appears to be between 2.01 and 3 for Kivircik ewes (Yilmaz et al., 2011). The optimum for the Lacaune ewes is not clearly referenced but the results obtained here imply that the BCS decrease, modelled in *BCS*− (−0.5 points out of the average), was not too drastic, so that in *BCS*− and *Ref*, the number of ewes reaching the optimal pre-mating BCS of the Lacaune breed was equivalent. In contrast, in *BCS*+, a larger number of ewes with optimal pre-mating BCS can be assumed. These results have also shown that two flocks with different individual characteristics appeared to have similar overall performance, suggesting that two management strategies leading to two different sheep flock structures could lead to the same flock performance. This confirms the relevance of the integration of individual characteristics in the REPROsheep model to examine ways of optimising reproduction management practices in dairy sheep flocks. Puillet et al. (2010a) suggested with their dairy goat model that taking individual performance into account in a herd functioning model is relevant and necessary for the evaluation of herd management practices, as the aggregation of individual data at the herd level can sometimes cover differences between management strategies. In this case, the nonsignificant difference at the flock level between the results of the *BCS*− and *Ref* scenarios suggests that the farmer could have a small margin to manoeuvre in the BCS maintenance of his ewes (e.g., through feeding management) without compromising the reproductive performance of his flock.

Overall, it was noted that the changes in performance observed within *BCS*+, *All*+ and *All*−, although significant, remained small, in regard to the total lambing rate of the flock (+1%, +3% and −3% on the total lambing rate for each scenario, respectively). Indeed, plausible flock scenarios for an organic farm of the Roquefort Basin were simulated, leading to fairly modest increases in average age and BCS modelled (0.5 BSC and/or 0.5 years, from a starting point of 2.5), with fairly low standard deviation for the pre-mating BCS (sd = 0.3). Thus, it should be acknowledged that with a more extreme flock population, results could have been different.

On the over hand, the effect observed on the distribution of lambing over time was much more noticeable. Indeed, *BCS*+ and *All*+ led to a better concentration of lambing during the first lambing period (P1) when compared to *Ref* (proportion of the total number of ewes lambing is higher by 6% and 13% for *BCS*+ and All+, respectively), accompanied by a better flock milk yield at the first peak of milking (peak 1) (+9% and +22% of milk produced in *BCS*+ and *All*+, respectively, compared to *Ref*). This suggests a better synchronisation of oestrus following ME. This is consistent with the positive effect of age, BCS and milk yield stated in the literature (Fahmy, 1989; Kassem et al., 1989; Maatoug-Ouzini et al., 2013; Kenyon et al., 2014; Debus et al., 2021). Similarly, the *All*− scenario led to a lower concentration of lambing during P1 and a lower milk yield at peak 1 (proportion of total lambing during P1 lower by 12% and 18% less milk produced at peak 1, compared to *Ref*), suggesting less oestrus synchronisation compared to *Ref*. Therefore, a significant effect of individual characteristics on lambing distribution over time was simulated, which confirms the suitability of the model with important management issues in sheep farming. It is true that lambing distribution over time is a determining factor in sheep farming, as it relates to other important issues such as work organisation, distribution of production and sales (of milk and lambs) or development of grassland and grazing resources (Cournut and Dedieu, 2000). It also accounts for the success or failure of the oestrus synchronisation method implemented by the farmer.

The REPROsheep model therefore seems relevant to predict how a management strategy (determining flock structure in terms of age, body condition or production potential) can impact the performance of a dairy sheep flock, particularly the distribution of lambing over time, in the context of reproduction on natural oestrus or even for the implementation of animal insemination. However, to draw accurate and definitive conclusions, the REPROsheep model would need to be applied to a wider range of different organic dairy sheep flocks. The outputs obtained and the conclusions drawn during the exploration of the REPROsheep model therefore remain theoretical and need to be confirmed by applying it to a larger number of farms managed without hormones as well as simulating several successive breeding campaigns (over several years). Indeed, a model allowing a simulation of successive breeding periods would require additional assumptions that were not included here, such as, for example, taking into account the genetic aspect in renewal choices, which could mean adding conditions in order to adapt the stated relationships to the modelled context. This aspect will have to be taken into account in a future version of the model to test the impact of the implementation of animal insemination in organic dairy sheep farming. It would make it possible, among other things, to precisely link the trends observed with flock management strategies and to assess the long-term impact of changes in practices or of innovative practices introduction in the context of sheep reproduction hormone-free management (Maton et al., 2014).

5. Conclusion

The REPROsheep model was interesting for studying the dynamic effects of implementing a hormone-free reproductive management strategy in a dairy sheep flock. It allowed us to assess flock level performance over time by considering particular individual performances of ewes composing the flock. This model therefore represents a tool to better understand mechanisms and trade-offs occurring in the interplay between the individual and flock levels, exacerbated (or not) by applying sheep reproduction management practices without hormones, for oestrus induction and synchronisation. Nevertheless, the flock management results obtained here, even if exploratory, suggested that management favouring an optimum pre- mating body condition score and age, as well as good milk yield in the individuals of the flock, might be a lever for optimising flock performance, especially the distribution of lambing over time. Further research is warranted to fully validate this hypothesis by applying the model to other hormone-free dairy sheep flocks and to perform simulations with a long-term perspective. It would also be interesting to conceive how the stated findings interact with the management of other components at the whole farming system level (and not just the flock) in the context of the agroecological transition of dairy sheep farming systems.

CRediT authorship contribution statement

E. Laclef: Conceptualization, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft. **N. Debus:** Conceptualization, Investigation, Methodology, Writing – review & editing. **P. Taillandier:** Conceptualization, Methodology, Software, Writing – review & editing. **E. González-García:** Conceptualization, Methodology, Writing – review & editing. **A. Lurette:** Conceptualization, Methodology, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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