Towards resilient livestock systems : a resource allocation approach to combine selection and management within the herd environment

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Towards resilient livestock systems: a resource allocation approach to combine selection and management within the herd environment

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GENERAL PRESENTATION

Chapter 1: INTRODUCTION

1 Context of the thesis

Livestock farming systems in the coming decades are inevitably going to involve trade-offs among food security, poverty, environmental sustainability and economic development (Thornton, 2010). These challenges will promote the development of new paradigms of production improvements because the production process relies on an increasing number of factors that can be highly variable and uncertain. In developed countries, intensive livestock farming systems are trapped between the need to innovate through the implementation of ecologically sound alternatives (Janzen, 2011; Dumont et al., 2013), and the need to manage the costs they incur and the risk they take while doing so. In this tension, a system focus is essential to appropriately evaluate and implement adaptation options at the farm level. These adaptation options should also consider the regional environment and the internal aspects of farms, and how farmers can effectively integrate them.

A core area of livestock systems research is to build management aids for livestock farmers and tools for advisors, based on a better understanding of herd functioning (Gibon et al., 1999). In this view, management practices have to be assessed not just in terms of their immediate action on animals in the herd and their responses, but also in terms of how these responses, in turn, affect management in the future. The need to represent the interaction between farmer’s decisions and the biotechnical system is becoming more and more obvious for the design of herd systems that are efficient and resilient to internal and external perturbations (Darnhofer et al., 2010a). A major challenge is thus not only to investigate the means of improving efficiency of biological and technical factors in the production process (e.g. turn feed inputs into milk product while minimizing wastes), but also those allowing for the regeneration of the capital and effective husbandry practices through time (Thompson and Nardone, 1999).

The choice of livestock germplasm is a major determinant of the production process as it involves different levels of organization –within herd and between herds– which can progress at different rates. Within the herd, livestock germplasm represents a biological capital, embodied and regenerated in the group of females that produce and reproduce, but it is equally a major input that can be imported into herds –often as males’ gametes– to achieve better productivity. It is thus an essential attribute of the herd production process as the combination of these two aspects constitutes the genetic basis from which performances are elaborated within the herd, and can be preserved or improved. However, between herds, there is not a unique way to achieve a genetic improvement that will contribute to the efficiency of a farm (Olesen et al., 2000). In the economic context of the farm, there might also be the alternative of saving inputs of production factors per unit product. In a highly uncertain environment, a top priority for farmers is not to get higher production levels per animal only, but rather to combine high productivity with improved functional traits that contribute to the long term sustainability of the production process, such as health, fertility, and feed intake capacity (Olesen et al., 2000). In this context, a major issue for genetic improvement organized at national level is to propose livestock germplasm adapted to the local farm conditions and satisfying the farmer's priorities.

In this thesis, the above issue was tackled from a herd system perspective. It was thus viewed the other way around, i.e. from the manager's viewpoint, with the concern of finding satisfying combinations of selection and production in the local management system. Before considering how managers can effectively integrate these aspects, we first describe the relation between genetic improvement and the herd environments.

2 On the relation between genetic improvement and herd environments

2.1 Success of adapting herd environments to improved genotypes

The livestock breeding industry is generally organized in a hierarchical manner with the seedstock selected and multiplied in a small number of elite herds and disseminated and used in most of the others herds, usually referred as commercial herds (Simm, 1998; Harris and Newman, 1994). This hierarchy is often viewed as a pyramid, where genetic improvement is generated during the successive rounds of selection in the top elite herds and then flows down to commercial breeders (Figure 1-1).

Under some conditions, the top-down organization of breeding schemes is highly effective in practice. At the level of elite herds, accurate predictions of the genetic merit in the trait of interest enable selection of animals that are genetically superior to their contemporaries. This usually occurs when the effects of genes have been effectively disentangled from the environmental effects, which is facilitated by the provision of environmental conditions favourable to gene expression (e.g. high nutrition, low pathogen load, neutral temperature). At the level of commercial herds, proper nutrition and management enable the high potential production of improved genotypes to be realized (Vandehaar and St-Pierre, 2006). For these herds, it is economically interesting to improve the genetic merit of their herd, as long as the associated benefits are greater than the supplementary costs to allow expression of this merit. Therefore, a favourable economic context of production stimulates the demand for improved genotype in commercial herds and strengthens the hierarchical implementation of breeding programs. Genetic progress becomes even faster when the programs are implemented on large scale, either regional or national, and when selection is practiced on a moderate number of traits that are easy to record either in selection candidates or their close relatives such as progeny. This is typically the case where the primary focus is to select for increased milk yield in dairy production, and there is no question that such programs have been working spectacularly well for many years (Hansen, 2000).

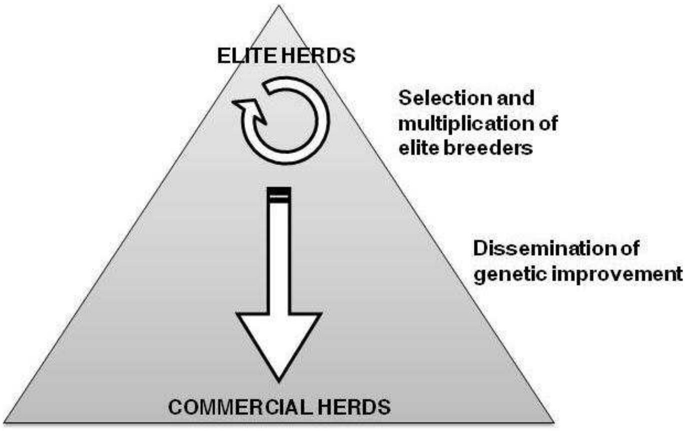

Figure 1-1 : Schematic representation of the structure of livestock breeding industry in developed countries. Adapted from Simm (1998).

When it is organized hierarchically, the relationship between genetic improvement and the commercial herd environments seems unilateral. The modernization of dairy herds has been characterized by important progress in technical efficiency due to major advances in nutrition, reproduction and mechanization. For instance, improvements in roughage quality and diet supplementation have increased the quantity of milk produced per kilogram of dry matter. Adoption of automated milking system diminishes the work load related to milking whilst increasing the milking frequency of dairy females which stimulates lactation (Svennersten-Sjaunja and Pettersson, 2008). Although these technologies often have disadvantages as well, the most efficient farms have been successful in reducing the cost of milk production (Kumbhakar et al., 1991). Genetic progress for milk yield (coming from the pyramidal organization) has thus likely been a key driver of many technical changes made by farmers. In effect, they have been adapting the herd environment to the improved genotypes, so as to keep up with genetic progress. However, achieving this seems increasingly complicated if production factors become increasingly variable and uncertain to manage in the herd environment.

2.2 Environmental limits and challenges emerging in the context of genetic improvement

From the early 90', it has been increasingly recognized that genetic progress in production together with improvements of environmental factors can not only lead to spectacular increases in production efficiency, but also to undesirable side-effects (Nebel and McGilliard, 1993; Rauw et al., 1998). When different genotypes are transferred from one environment to another –for instance from a high level of nutrition to a lower level– in some cases they can either rank differently for performance traits, or the differences between genotypes can become greater or lesser across environments (Simm, 1998). This situation, also termed genotype-by-environment interaction (**G × E**), is generally used as a way to quantify the animal adaption to the environment in which they have been selected. **Specialist** genotypes are deemed to express a high level of performance but in a narrow range of, largely non-constrained, environments. In contrast, **generalists** are deemed to perform moderately but over a wide range of environmental constraints (Kolmodin et al., 2003; Bryant et al., 2006; Strandberg et al., 2009). In practice, G × E have been suggested by differences between strains of Holstein cows or by the transfer of improved genotypes from temperate to tropical climates. Still, evidence of G×E effects such that animals re-rank for production traits are rarely found in genetic studies (Veerkamp et al., 2009); so in appearance, the best animals selected for high production remain the best whatever the environments in which they perform.

In the case of intensive dairy production systems, there is evidence that selecting only for milk yield traits can result in negative associations with other traits relative to reproductive longevity. This has been particularly apparent in dairy cattle through large scale observations of a decreasing trend for fertility (e.g. Lucy, 2001; Walsh et al., 2011) and through evidence of negative genetic correlations for milk yield with health and reproductive traits (e.g. Pryce et al., 1997). This indicates that further selection for increasing production can result in decreasing fertility or health, a situation that is sometimes described as a **trade-off** between life-functions, as defined in quantitative evolutionary genetics (in this case, the trade-off is defined by the response of populations to selection, i.e. there is genetic basis for the relationship between functions (Reznick, 1985; Stearns, 1992)).

Over time, conditions favourable to single-trait selection for milk production may become more and more compromised by the herd environment, even in environments where selection originally took place because there are limits such as those imposed by the rumen that cannot be easily overcome. Moreover, the increasing volatility in the price of concentrates can lead farmers to limit temporarily their use in feeding, especially when the sale prices are simultaneously low

(Lelyon et al., 2011). Extreme climatic events can also compromise the quality and the quantity of forages harvested in the farm or bought on local markets (Nardone et al., 2010). From these uncertainties, it is inevitable that the range of nutritional constraints within-farm will extend in the future. Options have thus to be found to select new genotypes that can face these conditions, while also maintaining improvements in farm efficiency.

Two approaches are generally available to match genotypes and environment; one is to act on the animal's environment so as to make it less constrictive for them (e.g. feed supplementation, use of reproduction techniques). The other one is to adapt animals at the genetic level so that they cope well with the variations in their environment. Although these two approaches are well recognized by both animal production scientists (e.g. Blanc et al., 2006) and geneticists (e.g. Huquet et al., 2012) they are generally considered separately. Before seeing how they might be integrated, we briefly describe where they can connect together.

2.3 Selection adjustments for matching genotypes to herds environments

An obvious selection adjustment to overcome the limits encountered with single-selection is to select on more than one trait (i.e. multi-trait selection). Multi-trait selection index are used to balance the selection emphasis on others traits of economic importance than solely production traits (Groen et al., 1997; Miglior et al., 2005). For this purpose, there has been a growing interest to record new traits and to develop reliable methods for estimating the parameters needed to predict selection response. Another possible selection adjustment is to define the environment and the selection criteria at a much finer-grained level of aggregation, especially because it can change the relative importance of traits. Once the environment has been characterized, customized indices can be used to indicate to farmers the best sires for their own herd conditions (Bowman et al., 1996). Although practical interest in using such indices instead of global or national indices is typically limited, it could become more attractive with the possibility to estimate more and more accurately environment-specific breeding values, based on animal trait measures and herd descriptors

Adjustments in the statistical methods used for genetic selection are likely to be effective for matching genotypes to herd environment. Part of their effectiveness, however, implies a trade-off between the accuracy of the estimated parameters used to make calculations (which generally require a substantial data set), and the customization of the selection index to accommodate the environmental particularities in which selection response takes place (Bourdon, 1998). The progress in computational power and the increasing quantity of information available on farm will probably help to overcome these difficulties in the future.

This opens promising perspectives for their integration into decision support tools that can help farmers. From this perspective, it would be crucial to carefully consider the role of the manager who sets the selection criteria and on-farm strategy, modulates or not the herd environment and can create "local" environments that match animal genetic expression through time.

2.4 Nutritional insights on adaptation

Short-term efficiency gains are largely achieved by an increase in production relative to non-productive functions (Veerkamp, 1998), i.e. there is an increased partition of nutrients towards milk. However, this change in partition has been shown to have unfavourable consequences on both reproduction and health status, in both cases to a large extent mediated by a decrease in body reserves (Rauw et al., 1998). The follow-on consequence of this is a decrease in longevity, and hence the length of the productive life of the animal. Thus, lifetime efficiency is decreased (because the productive portion of the lifespan declines). In this context, the adaptive capacity of animals and the role of nutrient partitioning are clearly important, especially with increasing environmental variability.

Two types of regulations in nutrient partitioning are now recognized (Friggens et al., 2013). **Homeostasis** refers to the regulations involved in the maintenance of the internal environment (Chilliard et al., 2000). They are directed to the survival of individual when they face some environmental disturbance, e.g. body reserves mobilization during underfeeding. Others regulations that have been less obvious among animal scientists are those referring to **teleophoresis** (Bauman and Currie, 1980; Chilliard, 1986; Friggens and Newbold, 2007). These regulations drive orchestrated changes of priority for the nutrient partitioning between functions and are directed towards the perpetuation of the specie. They are part of the genetic make-up of the animal, and their expression often explain why genetic correlation change for instance for body condition score during the stage of lactation (Pryce et al., 2001; Friggens, 2003). This clearly stresses an important connection between selection and nutrition. The modeling of teleophoretic and homeostatic regulations led to major advances in the prediction of multiple nutritional responses at the animal level (Sauvant, 1994; Martin and Sauvant, 2010). It represents also a strong conceptual basis to tackle the issue, as yet unexplored (Bryant et al., 2005), of integrating such animal model into a population/herd structure so as to test responses to selection.

2.5 Modeling as a tool for dealing with complexity

Modeling has been identified as a powerful tool for integrating complex relationships between genetic factors, the nutritional environment and time (McNamara, 2012). However, animal nutrition and genetic selection are classically viewed as separated models (Figure 1-2), probably because as they involve processes at different spatial and temporal scales. As previously mentioned, genetic improvement generally occurs at the level of national or regional populations. Based on the observed phenotypic traits of interest and on pedigree information, breeders select superior genotypes as parents (Figure 1-2A) and iterate the process over successive generations. By contrast, animal nutrition is practiced in individual herds with a wide range of different feeding systems often related to the local farm environment. Moreover, herd managers often adjust animal nutrition according to their short-term response and their reproductive stage as they know that animals change their nutrients partition between functions (Figure 1-2B).

Selection and nutrition operate thus at very different scales. Though, nutritional responses are well recognized as being regulated by genetic drives (Bauman and Currie, 1980; Chilliard et al., 2000). Theoretically, this component should be thus partly inherited from parents to offspring. In turn, within-life performances shape the response to selection, in particular through their effects on reproduction and survival rates. This suggests that the selection and the nutrition processes interact. A view that brings them together would be thus valuable at the herd level to provide more insights on how to take advantage of G × E interactions by the means of genetic selection and herd management (Figure 1-2C). This is clearly not a simple issue to address. Modeling represents a powerful tool to deal with such complexity; however it requires an appropriate theoretical basis to do so.

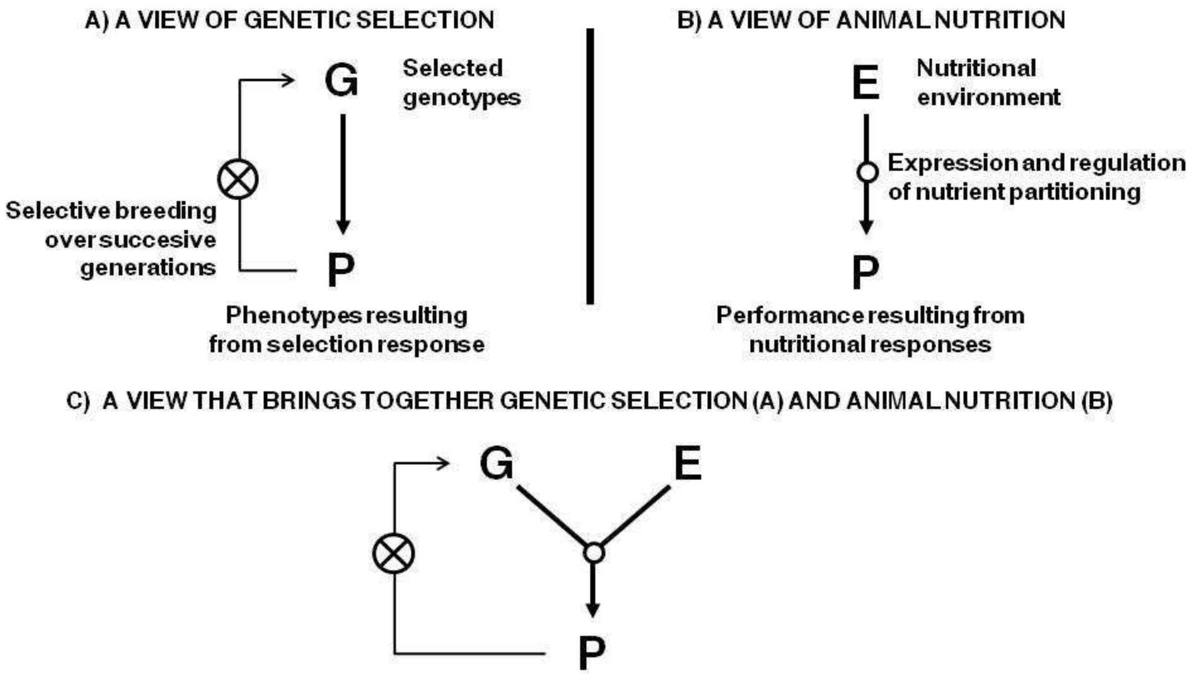

Figure 1-2: Two separates views of genetic selection (A) as an inter-generational process of selecting elite individuals among a population of candidates, and of animal nutrition (B), as an intra-generational process of nutrient partitioning by individuals. The emergence of G × E interactions can be viewed as a result of combining these two processes (C).

3 Managing G × E interactions at the herd level

3.1 The resource allocation approach

The integration of selective breeding and nutrient partitioning approaches to be able to manage and exploit G×E could benefit from other theoretical developments in biology. Resource allocation principles have been developed by evolutionary biologists who were interested in why some wild species are found in particular ecosystems, and how can it result from the interactions between natural selection and ecological processes (Williams, 1966; van Noordwijk and de Jong, 1986; Stearns, 1992). One aspect of the analogy with farm animal sciences is reflected in the terms "allocation" and "partitioning", which are effectively synonymous. A subtle difference however is that "allocation" refers to the action of assigning resource for a particular purpose whereas "partitioning" refers to the division into parts, without any notion of achieving specific functions. This difference underlines the explicit consideration, by life history scientists, of evolutionary "goals" for animals that seek to increase their natural fitness by the mean of possibly various "strategies". This conceptual distinction with a passive view of animal functioning traditionally held in animal nutrition has also emerged in animal science (Friggens and Newbold, 2007). The remaining aspect of the analogy lies in the parallel between individual natural fitness and the selection index used in selective breeding, as both reflect an adaptation measure of individuals to their environment but with a different weighting of traits. A central tenet of this thesis is that both aspects of the framework –resource allocation and natural fitness– can be applied and adapted to existing concepts in farm animal science –nutrient partitioning and selection index–, and thus provide an attractive way for connecting genetic selection and animal nutrition in a same view (Beilharz et al., 1993; Rauw et al., 1998; Friggens and Newbold, 2007; Rauw, 2009).

In life-history biology, resource allocation principles have been applied in a number of models to contribute insight into how the development of associations between traits can emanate from physiological constraints. The basic constraint which is postulated is that resources obtained from the environment are limited so that animals should find an optimal allocation between growth, reproduction and survival in order to maximize their fitness (Williams, 1966; Stearns, 1992). An interesting model outcome is that such physiological constraints are not always reflected in the observed phenotypes, and are therefore sometimes counter-intuitive (van Noordwijk and de Jong, 1986). This is illustrated in Figure 1-3 with a basic model of resource allocation, in which individual animals acquire a limited amount of resource (here called R) that they allocate in a given proportion (here called c) to one trait 1 and in the remaining proportion (1–c) to another trait 2 (right corner). The line in panel A represents a same level R of resource acquired at the population level. Different positions on this line reflect different allocation c between traits 1 and 2. Then, if animals vary more in their resource allocation than in their acquisition, traits compete for using the resource acquired and a negative correlation emerges (A). Conversely if animals vary more in the quantity of the resource acquired than in the way they allocate it between traits, a positive relationship between traits emerges (B). The important assumption here is the existence of a genetic variation in c which makes the link between the individual model and the population response across generations. Such a genetic variation is the basis of the selection response (Reznick, 1985).

The previous finding is particularly useful for breeding situations where one is interested in either selecting animals with favourable allocation or manipulating the nutritional environment in which the resource is obtained. From these theoretical considerations, it would be expected that a trade-off between traits would emerge as response to selection for trait 1 or 2, only if the nutritional environment limits the resource acquired (Beilharz et al., 1993). However it would require the quantification of genetic and environmental effects on the observed variations in acquisition and allocation parameters. A first step towards this objective has been applied with a similar model (Van Der Waaij, 2004), using a time-step of a generation. It has been found theoretically relevant regarding to selection (Bijma, 2009) and recognized as a good starting point for integrating genetic and nutritional factors (Friggens and Van Der Waaij, 2009).

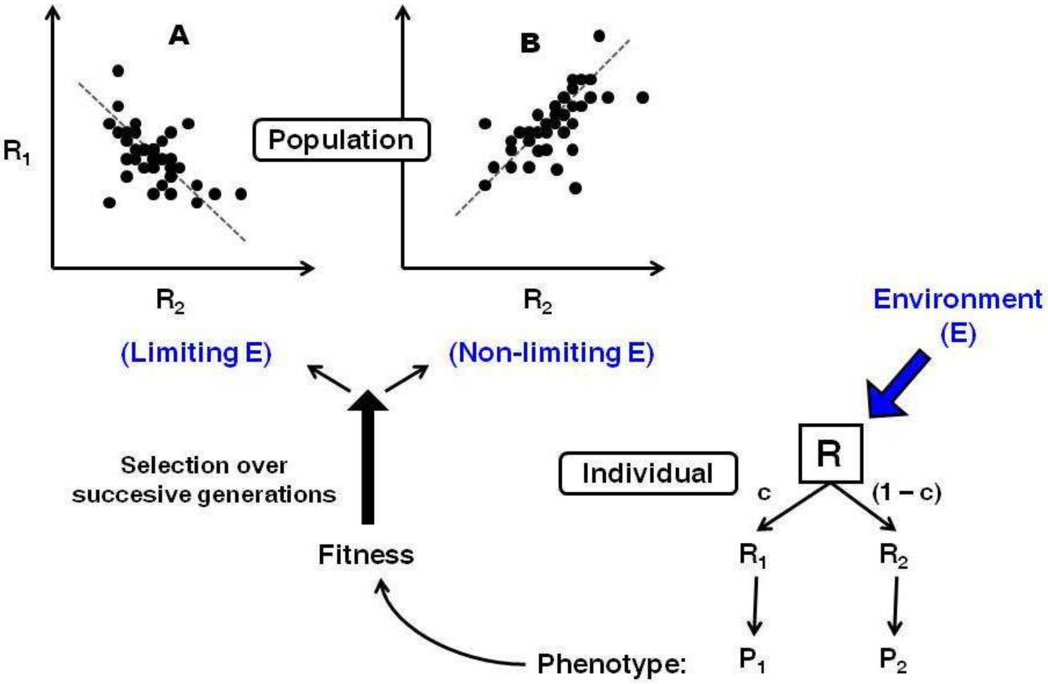

Figure 1-3: An individual model of resource allocation between two traits (A and B) and its consequences, at the population level, on the relations between traits and under two scenarios of variation in acquisition (R) and allocation (c). In population responses, each point represents one individual. Adapted from Van Noordwijk and De Jong (1986).

3.2 Herd management: a possible lever to alleviate trade-offs among traits

Because of the natural selection context for which they have been originally developed, resource allocation models generally have a coarse grain definition of animal environment both in space and time (Stearns, 1992). Seasonal variations of the environment are often assumed to limit the available resource for animals, which seems reasonable and apparently consistent with evolutionary strategies that can be found in wild species such as hibernation or migration. Domestication has considerably alleviated extrinsic limitations of the resource obtained (Beilharz and Nitter, 1998), by both improving the resource availability from the environment and by reducing the foraging effort. Moreover, for farm animals herd management determines the controlled environment in which animal performs and thereby may complicate the global herd response compared to the simple view proposed in Figure 1-3 (A and B).

Two main mechanisms influence the herd response. The first one concerns the emergence of herd properties from a variability of individual responses which can complement each other. This variability can directly result from voluntary decisions of the manager, for instance in terms of herd configuration. Dairy farmers can thus stabilize herd milk supply throughout the year by managing a diversity of lactation stages. With seasonal species such as goat, this can be done in spite of the innate reproductive seasonality, in particular through the use of daylight treatments. In others cases, the variability is an involuntarily consequence of herd management, mediated by the interaction with animal biology. For instance, the feeding plan, decided at a herd or group level, can create discrepancies between animal requirements and nutrient supply at the individual level. Interestingly, different feeding options can lead to the same level of efficiency but it involves different levels of biological solicitation (Puillet et al., 2011), thereby increasing the risk of involuntarily culling. In the past, individual variability was frequently considered as a positive attribute only for extensive systems, in particular with the use of different species (Tichit et al., 2004). Nowadays, there is a growing interest to study the advantages of managing individual variability in a larger spectrum of management situations (Tichit et al., 2011), including mono-specific intensive systems (André et al., 2010). The study of individual variability may thus benefit from the considerations of genetic differences and their change by the mean of genetic selection. A second mechanism concerns the cumulative long-term effects. It underpins the fact that effects of short-term decisions may not be reflected instantaneously in animal responses but only after certain time decay. Body reserves have an important role in these effects as they constitute the energetic capital that animals can either use to buffer nutrient variations in the environment or build to anticipate its use during high energy-demanding periods of their reproductive cycle, like in early lactation. Therefore, a strong biological investment during the current reproductive cycle, in terms of high mobilization or a low deposition of body reserves, can impair the performances of the future reproductive cycle (Walsh et al., 2011). There are feeding options which can take advantage of this capacity, especially for improving lifetime productivity (Rufino et al., 2009).

Sometimes there are good reasons to consider separately genetics and nutrition. The complexity of animal adaptation in herd systems suggests that there are also reasons to see how they interact (Figure 1-4). Herd management is more than just a provision of nutritional resource and the previous part suggests that some management opportunities could exist to alleviate trade-off between traits (due to the summed effects of individual responses or due the cumulative effects through time, or both). However, investigating these opportunities would require representing the biological variability which is generated within individual across lifetime (in response to feeding and reproduction management practices), and between successive generations (in response to the selection of individuals which produce and reproduce within the herd). To do so, a representation of the resource allocation process would require i) the incorporation of heritable traits that respond to selection, ii) the teleophoretic and homeostatic regulations that drive the resource allocation, and iii) the possible variations in the resource obtained, including those from the body reserves.

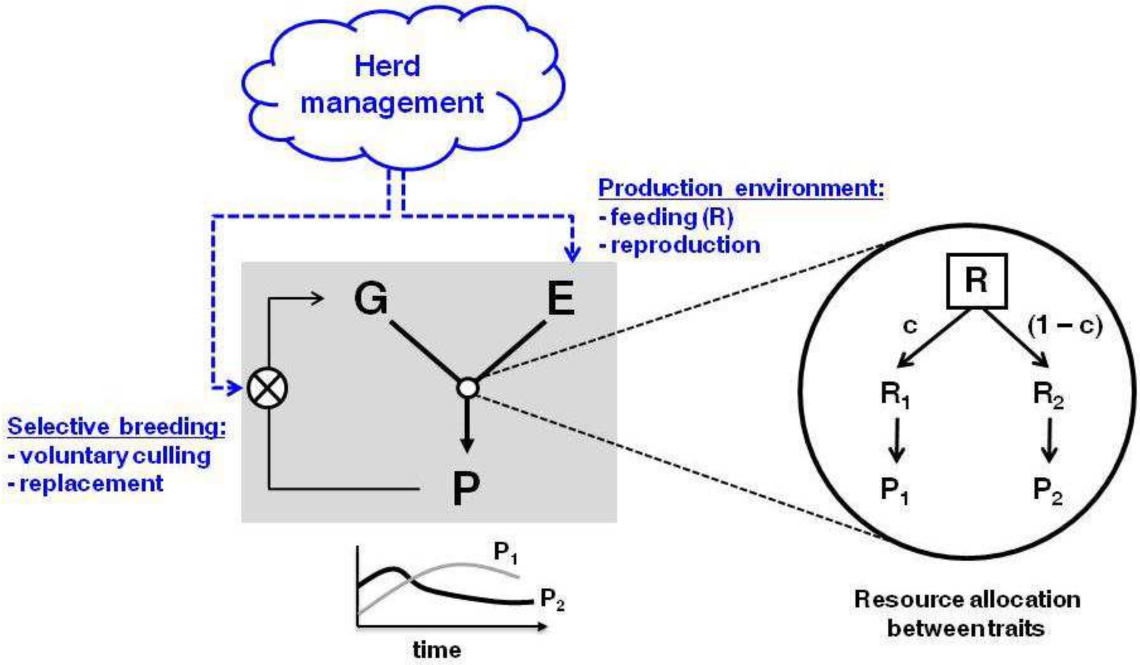

Figure 1-4: Influence of herd management on animal's resource allocation between the traits of performance. Animal's response to reproductive inputs activates the genetic drives of resource acquisition (R) and allocation (c) throughout its life. This is expressed in the time-profile of performance (P_1 and P_2), as a result of the genotype (G) interaction with the herd environment (E). Depending on their performance, some genotypes are selected to produce further in the herd whereas others are culled. Offspring of the best animal can also be selected to bring about genetic progress within the herd.

3.3 Interest for the design of sustainable systems

An important issue that arises with the idea of combining selection and herd management is why particular selection objectives would be suitable or not for a giving herd system. Herd systems exhibit a large diversity not only in terms of production environment (e.g. feeding system, geography), but equally in terms of objectives. Moreover, the global environment in which farms evolve may require global adjustment of the selection objectives for instance to accommodate a global change in climate (Nardone et al., 2010). Giving these conditions, an important practical issue would also be to determine the relevant scale for the design of sustainable selection objectives.

To address previous questions, an approach is to simulate the effects of farmer's management decisions on herd performance. However, this requires a credible farm decision model that is structured so as to be linked with an animal model. In particular, the animal model should be able to represent the possible constraints that emerge from the interaction between animal's biology and the herd production environment. These interactions have to be modeled over a span of time which makes sense with regard to sustainability criteria.

4 Research objective and case study

In this thesis, we propose that the management of G × E at the herd level requires a representation of animal's performance that integrates both the effects of selection and the effects of the herd production environment. The introduction above pointed out the potential interest of such integration for both genetics and animal production scientists but equally the conceptual challenge that it represents. Accordingly, the objective of this thesis was to **describe the elaboration of animal performance so as to explore the long-term consequences of the interaction between genetic selection and management within a herd.**

We previously pointed out the relevance of modeling as a tool to deal with the complexity of articulating the physiological and the genetic dimensions of animal performance. To tackle the issue, as yet unexplored, of incorporating genetic parameters within a nutritional model (Friggens and Newbold, 2007; Friggens et al., 2013), we elaborated on considerations from the resource allocation theory. Choosing this theory was motivated by the considerable available knowledge in the field of evolutionary biology, its importation and explanatory potential in livestock science (Beilharz et al., 1993; Rauw, 2009) and by the relevance of a previous model application (Van Der Waaij, 2004) as a starting point.

From a resource allocation perspective, a negative relationships between traits during selection results from functional relationship between these traits (Zera and Harshman, 2001). If they share a common pool of internal resources and if this pool is limited then a trade-off should emerge during selection for one trait because an increment of resource allocated for this necessitates a decrement of the resources allocated to the other trait. Clearly, others causes of negative relationships may exist such as genetic linkage or phylogenetic constraints (Stearns, 1992; Zera and Harshman, 2001). However, this is not under the scope of the resource allocation theory and the present thesis. Neither are the physiological causes (i.e. hormonal control) underlying the functional relationships between traits considered. Instead, the resource allocation theory used in this thesis focuses on illuminating the mechanisms of animal adaptation during the selection process. It aims to emphasize the functional relationships that constrain adaptation without, however, making explicit the underlying physiology.

Central to the thesis is the hypothesis that representing the effects of herd management on resource allocation would enable exploration of ways to overcome a potential trade-off between productive and functional traits (as described in Figure 1-3). In a limiting nutritional environment, herd management was investigated as a possible lever to alleviate trade-offs that would emerge during selection. For practical interest regarding both genetic selection and herd management, we decided to develop a sophisticated version of a resource allocation model based on previous modeling developments (Van Der Waaij, 2004; Friggens and Van Der Waaij, 2009).

As a case study, the animal model was developed and calibrated to the dairy goat. The management factor we chose was the use of extended lactation (EL). It can be defined as an extension of the lactation of non-pregnant dairy females beyond the normal standard lactation length (~ 300 d for both dairy goats and cows). The absence or delay of reproduction that should normally occur after parturition can be deliberately chosen by the farm manager or result from a reproductive failure after male exposure i. e. extended calving/kidding interval (Knight, 2001). This latter situation is often practiced in seasonal dairy cow production systems as an alternative to the culling of high yielding cows that failed to conceive during the annual reproductive period (Butler et al., 2010). A similar situation can be observed in dairy goat production systems although several crucial physiological differences exist relative to the cow. During the annual reproduction cycle of the dairy cow, the high energy requirements related to gestation normally compete with those of lactation which increases the risk of metabolic stress under limiting conditions. By contrast, the dairy goat conception normally occurs only in late lactation and is strongly controlled by seasonal factors (Chemineau et al., 2008) which reduce the possible interactions between gestation and lactation and their possible adverse consequences on health and future reproduction. However, in both species reproduction depends –to a different degree- on body reserves level and variations during the reproductive cycle (Friggens, 2003), which have been shown to be affected by selection primarily focused on milk yield improvement (e.g. Rauw et al., 1998; Dillon et al., 2006). The essence of EL is continued lactation at a metabolically sustainable level, therefore EL management of a proportion of the herd was expected to interact with genetic selection for production improvement (Knight, 2001). Due to reduced lifetime exposure to peak risk periods of metabolic stress and greater time to replenish body reserves, EL may be postulated to improve herd survival under selection for milk yield progress.

Extended lactation is increasingly described and understood in the dairy cow literature whereas it is still only partly described in the dairy goat. In particular, no studies allowed for a characterization of the dairy goat EL in terms of resource allocation between functions. However, the shape of the lactation curve observed in all studies suggests that a specific innate biological mechanism is involved during EL (Linzell, 1973; Salama et al., 2005; Chastin et al., 2001). Therefore, regulations of resource allocation different than those involved during a normal lactation may exist with consequences at the herd level.

Our research objective was then addressed in three steps:

i. What are the long-term effects of contrasting genetic selection strategies on herd performances?

ii. What is the time-profile of performance during EL and how does it fit the proposed modeling approach of resource allocation?

iii. What are the effects of interaction between contrasting selection strategies and the use of EL in herds subject to variations in the feeding level?

These steps are reported on the general approach adopted in this thesis (Figure 1-5). This approach was adapted from Giller et al., (2008) who situated the different roles of modeling in a research process that focuses on improving conceptual understanding. The model presented in this thesis is an half-way between simple models used to illustrate the explanatory potential of a theory (e.g. Van Der Waaij, 2004) and those that have been designed and calibrated to make more accurate predictions in the real world (e.g. Fox et al., 2004) . It has too many components for the first case and it is currently too limited for the second case. The model, and thus the level of description of the components, was designed for the purpose of scenario exploration (i). The model ability to accommodate new biological knowledge, here the effects of extending the lactation (ii) and to explore how does it interact with selection (iii) was also assessed.

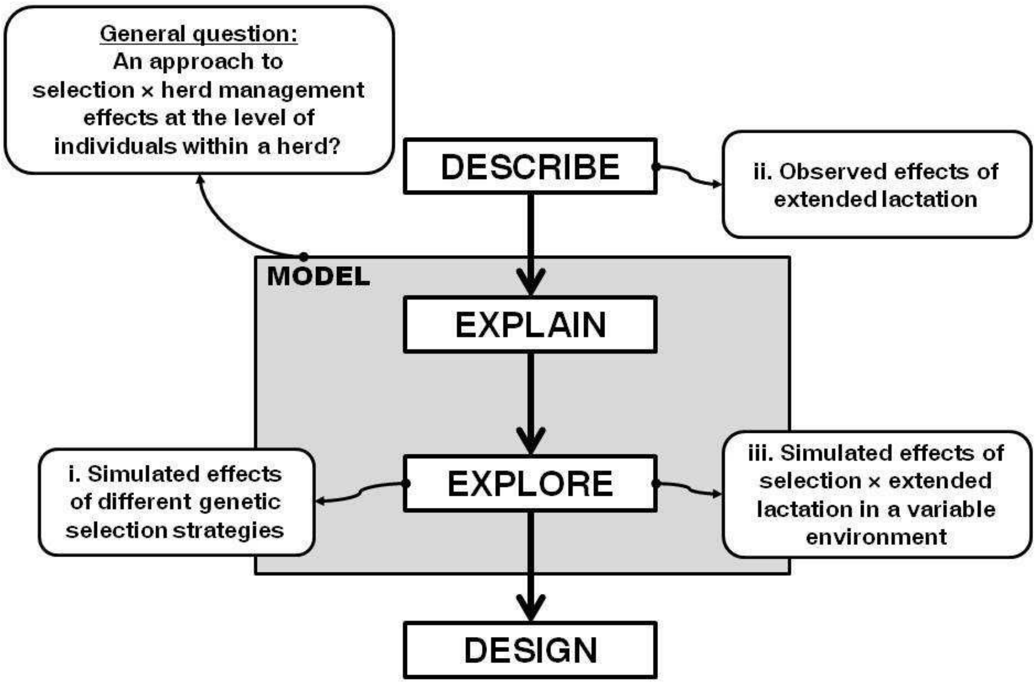

Figure 1-5 : General approach of the thesis (adapted from Giller et al., 2008) followed to answer the research questions

Chapter 2: GENERAL APPROACH

1 EXPLAIN: development of a herd simulation model

1.1 Model overview

Figure 2-1 presents the main processes that make up the herd simulation model developed in this study. The model was individual-based, discrete-time and combined a weekly cycle (left handside), which represents the nutrition process, with a yearly cycle (right handside), which represents selection and the mating processes.

The key point linking the two cycles was that every individual in the herd was characterized by heritable traits (**T_1, T_2, T_3**...) underlying the nutritional responses and thus affecting their weekly performance. Several traits (**P_1, P_2, P_3** ...) of this observed performance were recorded during year n−1 and used as criteria to select the individuals that will be parents in the next year n. Moreover, during the mating process, selected parents that reproduced successfully transmitted their heritable traits (T_1, T_2, T_3...) to their offspring.

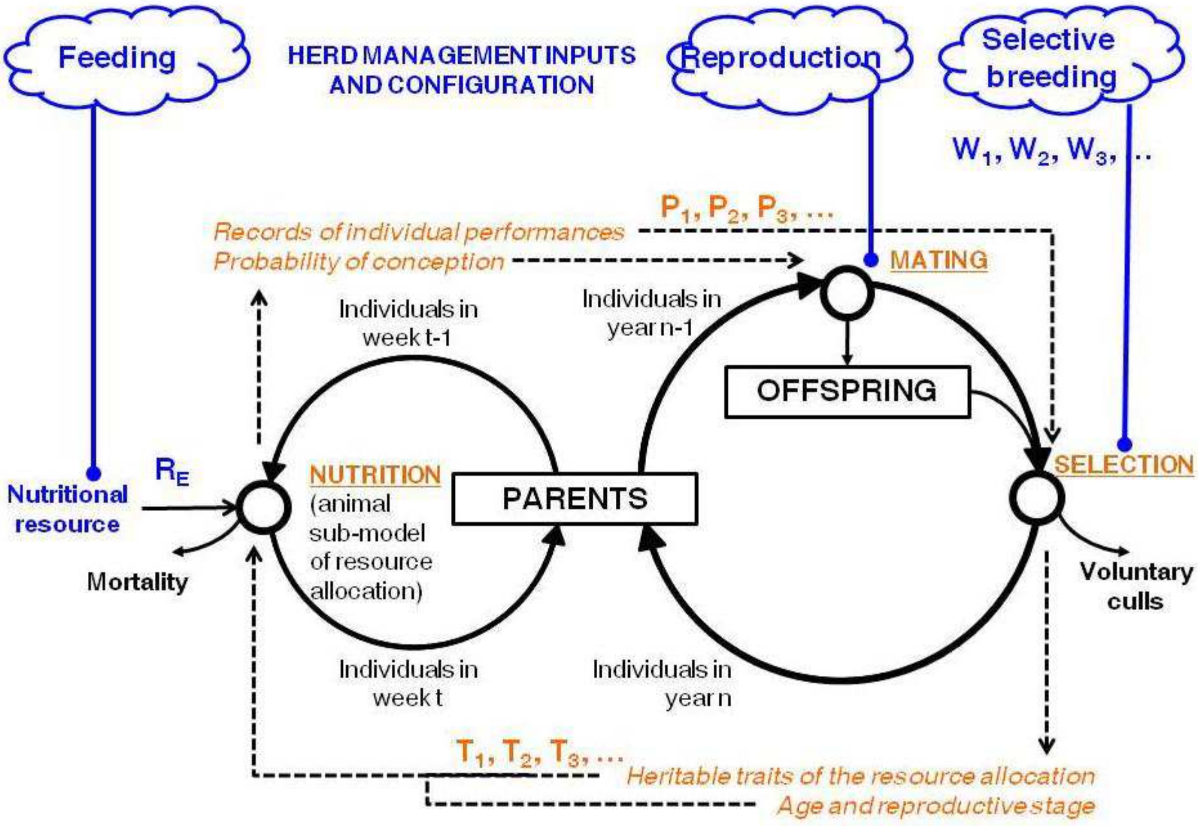

Figure 2-1 : Overview of the 3 main processes that make up the herd simulation model.

- ***Representation of Selection × Nutrition effects***

Once a year, surviving individuals were evaluated based on both i) criteria of observed phenotypic traits of performance and ii) the selection weights (**W_1, W_2, W_3** ...) defined in the manager's selective breeding strategy, and which reflect the importance given by the manager to the different traits. These weights were combined in a selection index (**SelIndex**) used to rank the candidates and select them. It was defined as follows:

$$\mathbf{SelIndex = (W_1 \times P_1) + (W_2 \times P_2) + (W_3 \times P_3) + ...}$$

Based on their SelIndex score, a fix proportion of the best candidates was selected to be parents in year n, the remaining proportion was voluntarily culled and replaced with the offspring born during the year. In the present study, young individuals chosen for replacements came from the herd and were sons and daughter of the elite adult females (those that had the greatest SelIndex, i.e. pedigree selection).

Nutrition was viewed at a high level of description, as a resource allocation process controlled by the underlying traits under genetic influence (T_1, T_2, T_3...). These traits were integral to allocation functions which vary with animal age and reproductive stage. Each week, a quantity of metabolizable energy was available in the herd environment (R_E) that allowed each individual animal to meet, to some degree, its desired intake (R_G), and then allocate it between biological functions (body reserves deposition, gestation, lactation, growth and survival). Based on these three inputs (i.e. the heritable traits of allocation, the resource available in the environment, and the age and reproductive stage), the nutritional responses obtained as outputs were describing a phenotypic variability in survival (i.e. risk of mortality), reproduction (i.e. likelihood of conception which determines the reproductive success during mating) and performance (i.e. partly used to calculate the criteria P_1, P_2, P_3 ...).

Overall, parent's selection and their replacement (reflecting part of the manager's priorities) along with inherent variation in individual survival and fertility (reflecting part of the animal's priorities) bring about genetic progress in the herd.

1.2 Animal sub-model of resource acquisition – allocation

The animal sub-model is described as a two-step process; first the acquisition of the resource from the environment, and possibly from body reserves, then the allocation of the total amount of resource obtained between biological functions.

- **Resource acquisition**

State-based relationships were assumed to describe the desired intake R_G. For a given week t, R_G was determined by the animal state (body size and fatness) the week before (t−1). This desired intake was positively related to animal size, here approximated by the non-labile body weight (**BWnl**, kg). In addition, R_G was adjusted according to body fatness, here approximated by the body condition score (**BCS**, 0 to 5 points scale). It was assumed that animals adjust their R_G to defend a target level of body fatness (**BCS***) (Tolkamp et al., 2006). When BCS was greater than the target level BCS*, body fatness had an effect of decreasing R_G and when BCS was less than BCS*, R_G was increased.

To satisfy its desired intake the animal could obtain resource from the environment ($Robt_E$) and from its body reserves (Rmob). The total resource obtained (Robt) was then allocated between the different biological functions and determines the new animal state at week t.

For each animal, the resource obtained from the environment ($Robt_E$) depended on the quantity of the diet available and its quality. In this study, the diet quality remained unchanged and was considered high. It was represented by a global diet quality factor, $\mathbf{Q_E}$ (between 0 (poor) and 1 (excellent), here equal to 0.85). This factor defined the proportion of R_G obtained by the animal when the diet was provided ad libitum. The desired intake obtainable was thus equal to the product $R_G \times Q_E$. However, the quantity of resource effectively obtained from the environment ($Robt_E$) could be less when the resource availability (R_E) was limited. We assumed that the amount $Robt_E$ was determined by the most limiting factor:

$$\mathbf{Robt_E = min\ ((R_G \times Q_E), R_E)}$$

The resource availability, R_E, was defined at the level of a class of animals (basically 2 classes being either less or more than one year of age), according to the proportion P_{LIM} (between 0 and 1) of this group not fed ad libitum. For instance, if P_{LIM} was equal to 0.75 then R_E was equal to 75th percentile of the distribution of the desired intake obtainable ($R_G \times Q_E$) (Figure 2-2). In this case, 75% of the animals would be fed ad libitum (for them $Robt_E = R_G \times Q_E$) and the 25% with the greatest $R_G \times Q_E$ would be limited by the resource availability (for them $Robt_E = R_E$).

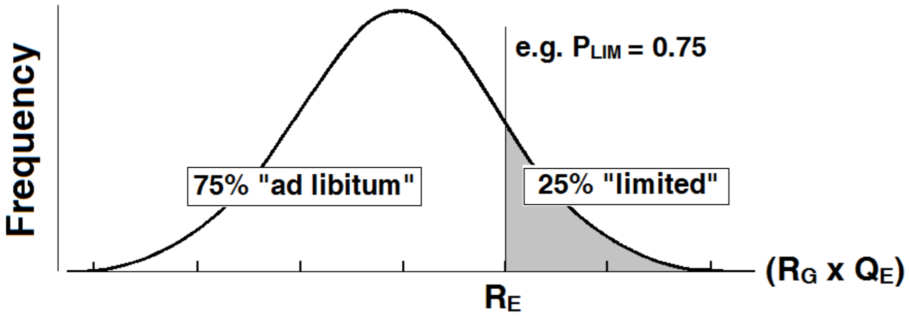

Figure 2-2 : Illustration of the determination of the resource available R_E at one time-step (a week) of the model. The curve represents a fictive distribution of the desired intake obtainable ($R_G \times Q_E$) of individual animals within a herd

When the resource $Robt_E$ was low compared to the desired intake R_G, animals could use their body reserves to partly compensate for the deficit (RmobE). Moreover, a genetically driven use of body reserves after parturition was also assumed (RmobG) (Chilliard et al., 2000; Friggens et al., 2004). The total energy obtained from the body reserves and the environment (Robt) was then allocated between the different biological functions.

- **Resource allocation**

Starting from an elementary representation of resource allocation such as depicted in Figure 1-3, the heritable traits (T_1, T_2, T_3...) were set at the level of the coefficients of allocation (c). We thus assumed a genetic control on the proportion of resource allocated between biological functions.

As resource allocation varies both in response to the stages of life and reproduction and to the nutritional environment, we further decomposed the c coefficient into i) a constant genetic component during lifetime (**c_0**) which was modified by ii) a time-component (**$cmod_G$**, between 0 and 1) and iii) an environmentally driven component (**$cmod_E$** between 0 and 1). These components were assumed to be multiplicative in the following general model:

$$c = c_0 \times cmod_G \times cmod_E$$

The $cmod_G$ component represented the temporal (t) changes in relative priorities between life-functions (Martin and Sauvant, 2010). The $cmod_E$ component represented the changes in allocation in response to the degree of satisfaction of the desired intake (**SAT**) (see details in Paper 1).

To represent a hierarchy of biological functions, the elementary representation of resource allocation was repeated at successive levels. Once the Robt has been determined, the model allocated it between body reserves deposition (**Rdep**), pregnancy (**Rpreg**), lactation (**Rlact**), growth (**Rgrow**) and survival (**Rsurv**). At each level of the hierarchy, the allocation coefficients **d**, **p**, **l** and **g** were constructed according to the general model (c). Thus, a proportion (c) of the resource available for allocation at one level (R) was allocated to the function at that level, whereas the remaining part ((1 – c) × R) was available for allocation at the next level down.

In the chosen hierarchy, the 5 different functions were ranked according to their degree of dependency on the nutritional environment. Body reserves deposition and pregnancy were considered to be quite dependant on the environment (they are activated only when the conditions are favourable) whereas growth and survival were considered as necessary functions (they are activated whatever the environment). When the actual intake was low compared to the desired intake (i.e. when SAT was low), survival was potentially compromised. In this case, a decrease in $cmod_E$ ($cmod_E \rightarrow 0$) allowed for resource reallocation towards survival (see details in Paper 1).

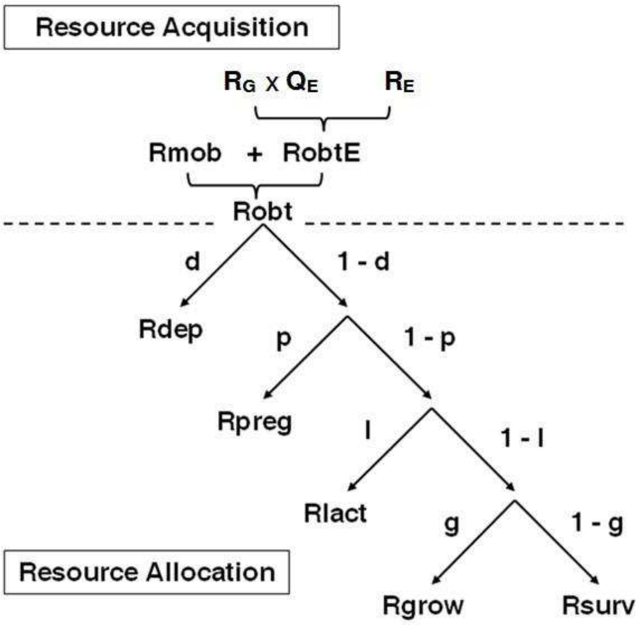

Figure 2-3 : Schematic representation of the resource acquisition process and the hierarchy of resource allocation between functions.

Every time step, the quantity of resource mobilized from the body reserves (Rmob) and the quanity of resource allocated (Rdep, Rpreg, Rlact, Rgrow and Rsurv) were used to determine the animal sub-model outputs (i.e. the phenotypic trait of performance). Energy corrected milk yield (MYcor, in kg/d), and changes in the mass of BWnl, BR and of the gravid uterus were calculated from the different amounts of energy allocated (Rlact, Rpreg, Rgrow and Rdep) and the total energy mobilized (i.e. RmobE + RmobG), assuming constant ME conversion factors. In particular, the variations in BWnl (from Rgrow) and in body reserves (from Rmob and Rdep) resulted in a change in body size (BWnl) and fatness (BCS) that affected the desired intake R_G at the next time step.

Survival was stochastically determined from a survival likelihood (**LSURV**). This likelihood was sigmoid, transiting from a low (0) to a high (1) level when the resource allocated Rsurv was increased relative to a basic level **$Rsurv_0$**. A standardization of Rsurv with respect to $BWnl^{0.75}$ was undertaken (**$Rsurv_{st}$**) to account for the effects of body size on the costs of maintenance. Additionally, an age-dependent term was introduced to reflect animal senescence as characterized by an exponential rate of decrease (**kage**). The LSURV likelihood was defined as follows:

$$\mathbf{LSURV = (1 / (1 + exp(- 15 \times (Rsurv_{st} - Rsurv_0))) \times exp(- kage \times age).}$$

Conception was stochastically determined from a conception likelihood (**LCONC**) following the approach proposed by Friggens and Chagunda (2005). The main determinants of LCONC were the BCS level relative to a base level, **BCS_0**, and a modification to this base level determined by the rate of change in body reserves (**dBR**) proportionally to some scaling factor (Xd_{BR}):

$$\mathbf{LCONC = 1 / (1 + exp(- 2 \times (BCS - (BCS_0 - X_{dBR} \times dBR)).}$$

2 DESCRIBE: a time-profile of dairy goat performance

2.1 Model calibration on a meta-profile

Parameters of the animal sub-model described in the previous section were calibrated with average data for a dairy goat fed ad libitum with a high quality diet (Figure 2-4).

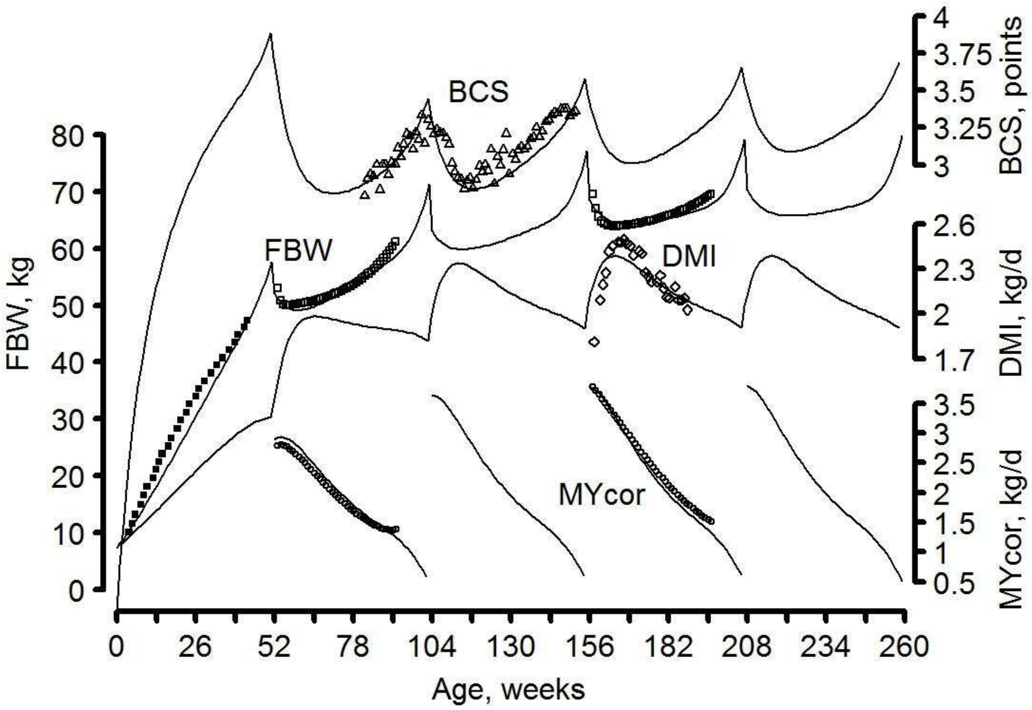

Figure 2-4 : Model simulations (continuous lines) of full BW (FBW), BCS, and energy corrected milk yield (MYcor) from birth to 5 years (i.e. 260 weeks) of life. Symbols are data used for model calibration: Sauvant et al., 2012 (○ and □); Puillet, 2010 (■); Sauvant and Morand-Fehr, 1982 (◊); Douhard et al., unpublished data (Δ).

2.2 Description of extended lactation from real data

To characterize the time-profile in the dairy goat undergoing EL some data was available in the literature (Linzell, 1973; Chastin et al., 2001; Salama et al., 2005). All of them suggested that an additional mechanism was involved during EL but this aspect was not elaborated in these studies. As EL is increasingly considered in the management of dairy goat systems, a better characterization had practical interest. For these reasons, we designed an experimental study to compare the effects of EL with a normal lactation and to characterize the relationships between milk production, live weight and intake that are associated with the EL profile (Paper 2). A specific objective was to characterize which one among these animal factors drives the others.

Based on this characterization, the EL aspect was included in the model so as to investigate the management possibility to compensate for reproductive failure by allowing EL.

3 EXPLORE: Simulation experiments

3.1 Description of G and E in the scenarios

- **Implementation of genetic variation (G)**

The allocation parameters considered as traits under genetic influence (T_1, T_2...) were implemented at the level of the allocation coefficients for body reserves deposition (d) and lactation (l). The basic components, $\mathbf{d_0}$ and $\mathbf{l_0}$ respectively, were chosen to represent variation in the genetically driven part of the allocation (Paper 1). Phenotypic population means were 0.25 and 0.75 respectively for d_0 and l_0. A phenotypic SD of 0.05 and a h^2 of 0.3 were used for these 2 traits. Initial true breeding values (TBV) of these traits were simulated in a base population and TBV of any new individual were then simulated from those of their parents.

- **Configuration of the herd environment (E)**

The level of variability in the resource availability was defined both between years and within year. For each year, an average yearly level of environmental limitation was sampled from a uniform distribution between a minimum P_{LIM} value (P_{LIM0}, here equal to 0.25) and 1. For each week (t) within a year n, the level of environmental limitation was sampled from a normal distribution with the average yearly level and a standard deviation (SD_{PLIM}, here equal to 0.15).

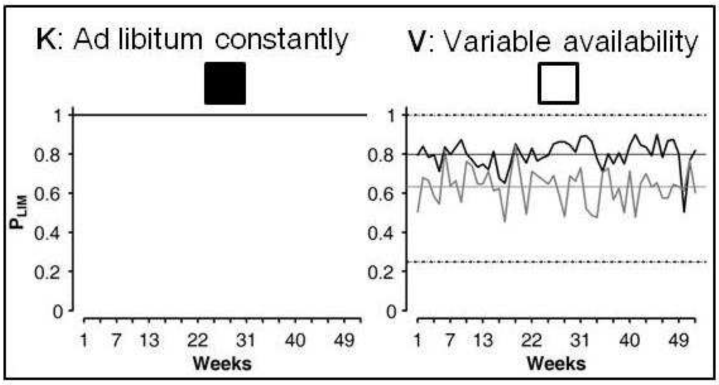

Figure 2-5 : Definition of environment variability

3.2 Scenario simulated of G × E

As a whole, the model accounted for 3 sources of individual variability that depended on herd management inputs (Figure 2-1): **i) genetic variability** implemented at the level of the resource allocation and which depends on the selection weights (W_1, W_2, W_3...) used in the selective breeding strategy, **ii) environmental variations** modeled through the level of the nutritional resource available in the herd environment (R_E) and **iii) time variations** between individuals due to differences of ages or reproductive stages depending on the rate of voluntary culling used in the selective breeding strategy and the possibility or not for goats to undergo EL.

The genetic component of individual variability was first explored. For this, we tested contrasting selection strategies while restricting the environmental influence. Selection was practiced in the K environment (Figure 2-5) and herd management was configured to restrict individual variability related to differences of ages or reproductive stage. In particular, females that failed to reproduce during the year were automatically culled at the end of the year when selection occurred (no possibility for extended lactation). Environmental variations were then considered with the V environment together with the time variations associated with the possibility to use EL to compensate for reproductive failures.

- ***The phenotypic criteria*** (P_1, P_2, P_3 …) that were recorded during the year and used in the SelIndex were the peak milk yield (MILK) the average BCS and BW, and the age of the animal at the moment when selection took place. Moreover, the reproductive status was considered in the V environment with the binary variable PREG (equal to 1 when the females was pregnant and -1 else).
- ***The selection weights*** (W_1, W_2, W_3 …) were defined relative to the above phenotypic criteria.

The strategies reported in this thesis were broadly defined according to the K and V environment. They are summarized in Table 2-1.

Table 2-1 : Scenarios simulated (grey zones indicate the selection weights used in the scenario; crosses indicate where a focus has been done by exploring different weighting for the criteria considered)

	Selection strategy				**Extended lactation**
Environment	+ BCS	+AGE	**MILK**	-BW	**(PREG)**
K	▨	▨	▨	**X**	No
V		**X**	▨		Yes

In the K environment, three contrasting strategies were explored :

- Selection for milk yield only (**S_Y**): $W_{BCS} = 0$; $W_{AGE} = 0$; $W_{MILK} = 1$; $W_{BW} = 0$

- Selection for milk production efficiency[1] (**S_E**): $W_{BCS} = 0$; $W_{AGE} = 0$; $W_{MILK} = 1$; $W_{BW} = -0.75$

- Multi-trait selection (**S_M**): $W_{BCS} = 0.5$; $W_{AGE} = 0.5$; $W_{MILK} = 1$; $W_{BW} = 0$

---

[1] This way of selecting for efficiency was slightly different from that used in Paper 1 where efficiency was approximated with the ratio MILK/BW. The way suggested seems closer to the way used in practice. Further it allowed defining a selection continuum between S_Y and S_E according to the value taken by W_{BW}. This latter part was explored in section 1.2 of the Results chapter.

The strategy to improve milk production efficiency was to select for high milk yield (MILK) while imposing simultaneously some penalty on BW. A similar strategy is often used in breeding programs aiming improvement in efficiency. To some extent the K environment reflect some intensive situations where a high quality feed is distributed at a high and constant level. In such a situation, a top priority for managers is get high milk production while moderating the feed costs. A focus on such a strategy was done by exploring the consequence of different weighting penalties on BW (S_E strategy with W_{BW} ranging from 0, 0.5,0.75, 0.85, 1).

In the V environment, 5 different selection strategies were defined with different selection weights on age (W_{AGE} = 0, 0.05, 0.10, 0.25, 0.50) to study the effect of an increasing emphasis on longevity for the 2 scenarios simulated (details in Paper 3). In all cases, the weights on MILK and PREG remained the same, with values of 1 and 1 respectively. We hypothesized that selection solely for MILK would be more risky in terms of survival than in the K environment. In this case, a top priority for the manager, in addition to production, might be to breed animals able to withstand periods of food scarcity. Selection for both milk and longevity (through age) was assumed to represent such an ability. Moreover, EL was also hypothesized as a means to increase longevity provided that lactating females that failed to reproduce had a chance to stay in the herd.

Model initialization and parameterization

The model started out with a newborn base population, and initialization was undertaken for a period of 20 years in a K environment with a fixed replacement rate to keep a constant herd size. For this initialization period, voluntary culls were chosen randomly allowing equilibrium in both herd demography, as well as in average performances, to be established.

The different strategies were simulated for 40 years with 20 herds replicated in each one. Performance based voluntary culling was set at a constant rate of 25% during selection. The number of replacements was determined to keep the total herd size constant (i.e. the number of individuals just after selection), here set at 500 females and 10 males. The 10 males were fully replaced every year.

Chapter 3: RESULTS

The results are described according to the three sub-questions of the thesis adressed in Figure 1-5. In an abundant environment, we report the long-term consequences of contrasted selection strategies before focusing on the consequences of a varying manager's priority for milk production efficiency. Results of this part were obtained by simulation without allowing EL in the herd (i.e. females that failed to reproduce during the year were automatically culled at the end of the year when selection occured). A characterization of EL based on real data is then proposed. With this aspect incorporated in the model, we finally report the consequences of selecting for milk and longevity in a variable environment.

1 Exploring different selection strategies in an abundant environment

1.1 Contrasted strategies tailored different resource allocation

Long-term selection responses in the K environment illustrated the model sensitivity to the contrasted selection strategies S_Y, S_E and S_M. Figure 3-1 shows the average performances of the selected dams in the herds. The underlying changes in the traits of resource allocation for lactation (l_0) and for body reserves deposition (d_0) are presented in Figure 3-2. The consequences of a progress in MILK on the survival rate and the reproduction rate are shown in Figure 3-3.

The three selection strategies led to an improvement in MILK but relied on different paths to do so. When selection was for MILK only (S_Y), animals were thus selected regardless of any other trait. The major consequence was that big and lean animals were preferred. Indeed, in these animals increasing desired intake emerged as the mean to get an high MILK. The decreasing trend for BCS was associated with a decrease in the resource allocation for body reserves deposition, (d_0), in favour of the subsequent allocations in the hierarchy (i.e. pregnancy, lactation, growth and survival, see Figure 2-3). In this case, a moderate pressure was imposed on the resource allocation for lactation l_0. When selection was for milk production efficiency only (S_E), big animals were penalized unless they had a really high value of MILK. Consequently, BW did not increased throughout the time of selection. In this case, the resources for body reserves deposition were massively reallocated towards lactation, i.e. a strong pressure was imposed on l_0. This was consistent with a high management priority for efficiency with an increasing amount of the energy obtained by animals being directly transferred from feed to milk. Finally, when selection was for MILK, AGE and BCS (S_M), the AGE and the level of body fatness remained almost unchanged compared to their initial value. However, the final level of MILK progress was notably lower than the two strategies aiming solely at a production improvement (although it had a similar rate during the first years of selection). This limited progress points out the limit of an improvement solely based on home-bred genotypes, as was assumed in the model.

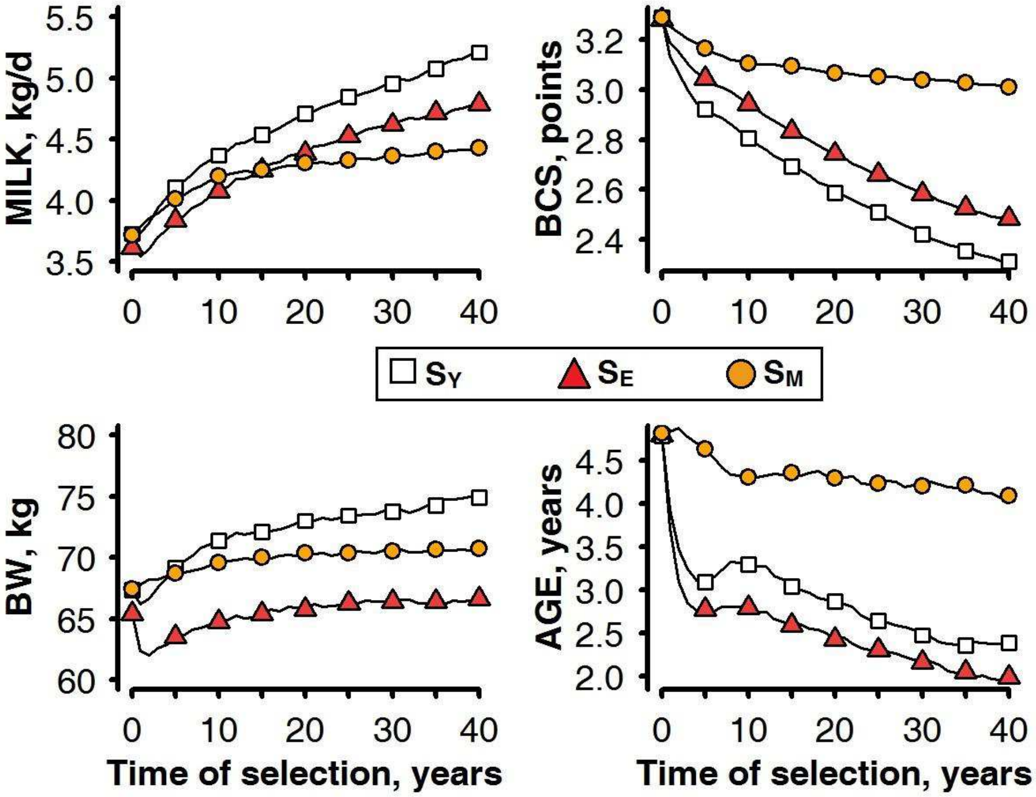

Figure 3-1 : Changes in average values of corrected milk yield at peak lactation (MILK), mean BCS (BCS), full BW at parturition (BW) and age (AGE) for the candidate females selected over 40 years in a favourable herd environment. Selection is for milk yield only (S_Y), for milk production efficiency only (S_E, with the ratio MILK / BW as a criteria of production efficiency), or for milk yield, body condition and age (S_M). Starting values were the result of a stabilizing period of random culling during 20 years before the 40 years shown during which selection strategies were applied.

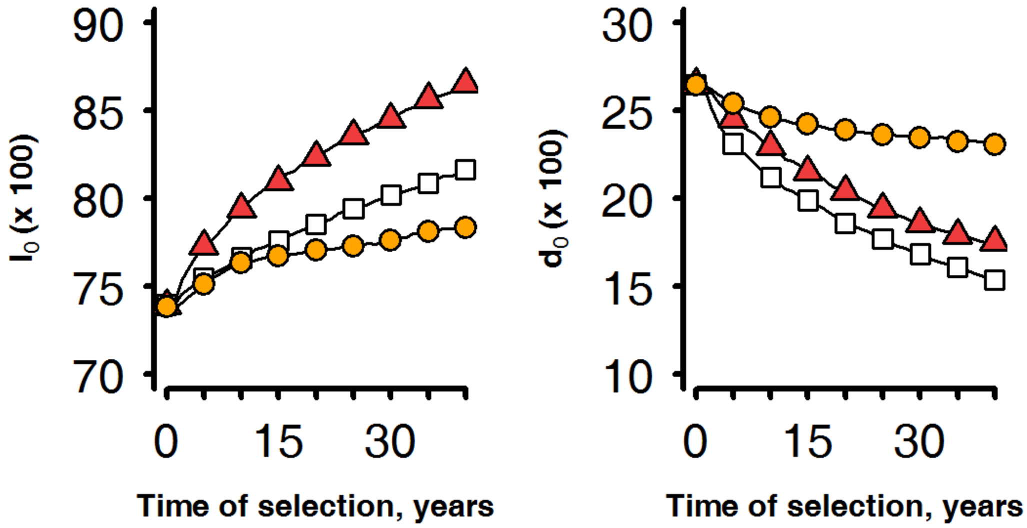

Figure 3-2 : Trajectories of the heritable trait of resource allocation for lactation (l_0) and that of body reserve deposition (d_0) for 3 different selection strategies during 40 years of selection in a favourable environment (each rightward progression reflecting 4 years of selection. Selection is for milk yield only (S_Y; white square), for milk production efficiency only (S_E; red triangle, with the ratio MILK / BW as a criteria of production efficiency), or for milk yield, body condition and age (S_M; orange circle). Starting values were the result of a stabilizing period of random culling during 20 years before the 40 years shown during which selection strategies were applied.

Figure 3-3 shows that even if the environment was nutrient-rich with unlimited resource availability, selection strategies aiming solely at a production improvement were risky in terms of survival or reproduction, or both. When a moderate pressure was applied on l_0 (S_Y), survival was not compromised as enough resource could be allocated to survival and compensate for the high cost of maintenance of these large females. This was not the case when a high pressure was applied on l_0 (S_E). In both cases, the depreciation of body reserves deposition strongly affected the rate of reproductive success (REPRO). This was largely determined by the relationship assumed between body fatness and the conception likelihood. In both cases, these consequences on SURV and REPRO considerable increased the level of culling due to biological reasons. Even if females from S_Y survived well, their probability to conceive was so low that they were often quickly culled for reproductive reasons. This explained why despite the differences depicted in Figure 3-3, the value of AGE was similar between S_Y and S_E in Figure 2-3.

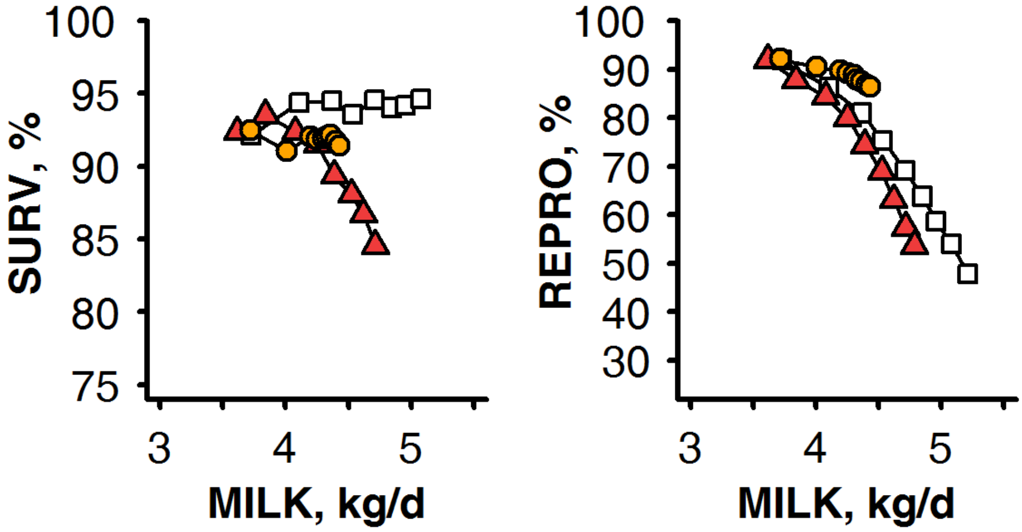

Figure 3-3 : Trajectories of herd survival rate (SURV) and reproduction rate (REPRO) relatively to average progress in milk yield at peak lactation during 40 years of selection in a favourable environment (each rightward progression reflecting 4 years of selection. Selection is for milk yield only (S_Y; white square), for milk production efficiency only (S_E; red triangle, with the ratio MILK / BW as a criteria of production efficiency), or for milk yield, body condition and age (S_M; orange circle). Starting values were the result of a stabilizing period of random culling during 20 years before the 40 years shown during which selection strategies were applied.

1.2 Consequences of a varying manager's priority for milk production efficiency

The relationship between SURV and MILK observed in Figure 3-3 was then investigated in terms of trade-offs. From Figure 3-3, it was expected that an increasing selection manager's priority for milk production efficiency would result in a linear decrease in SURV. To test this expectation, we compared the results of varying penalty on BW in the selection index (5 strategies with W_{BW} equal to 0 (i.e. S_Y), -0.5, -0.75 (i.e.S_E), -0.85 and -1). For each strategy, the average value of the last year is shown together with its 20 replicates (Figure 3-4).

We showed that a strong selection for milk production efficiency considerably reduced both the MILK production and SURV (Figure 3-4A). Therefore, the MILK loss due to a lower feed consumption (lower BW) was not compensated by a higher proportion of this feed being allocated to lactation. When starting to penalize BW from the S_Y strategy, a trade-off emerged with survival (Figure 3-4B, grey line): any improvement in efficiency incured a decrease in survival. Moreover, when the penalty on BW was too strong (≥ 0.85) selecting for high efficiency led to the opposite effect, i.e. reducing it, because of a dramatic decrease in survival. This non-linear change was reflected in the changes of the heritable traits of resource allocation l_0 and d_0 (Figure 3-5).

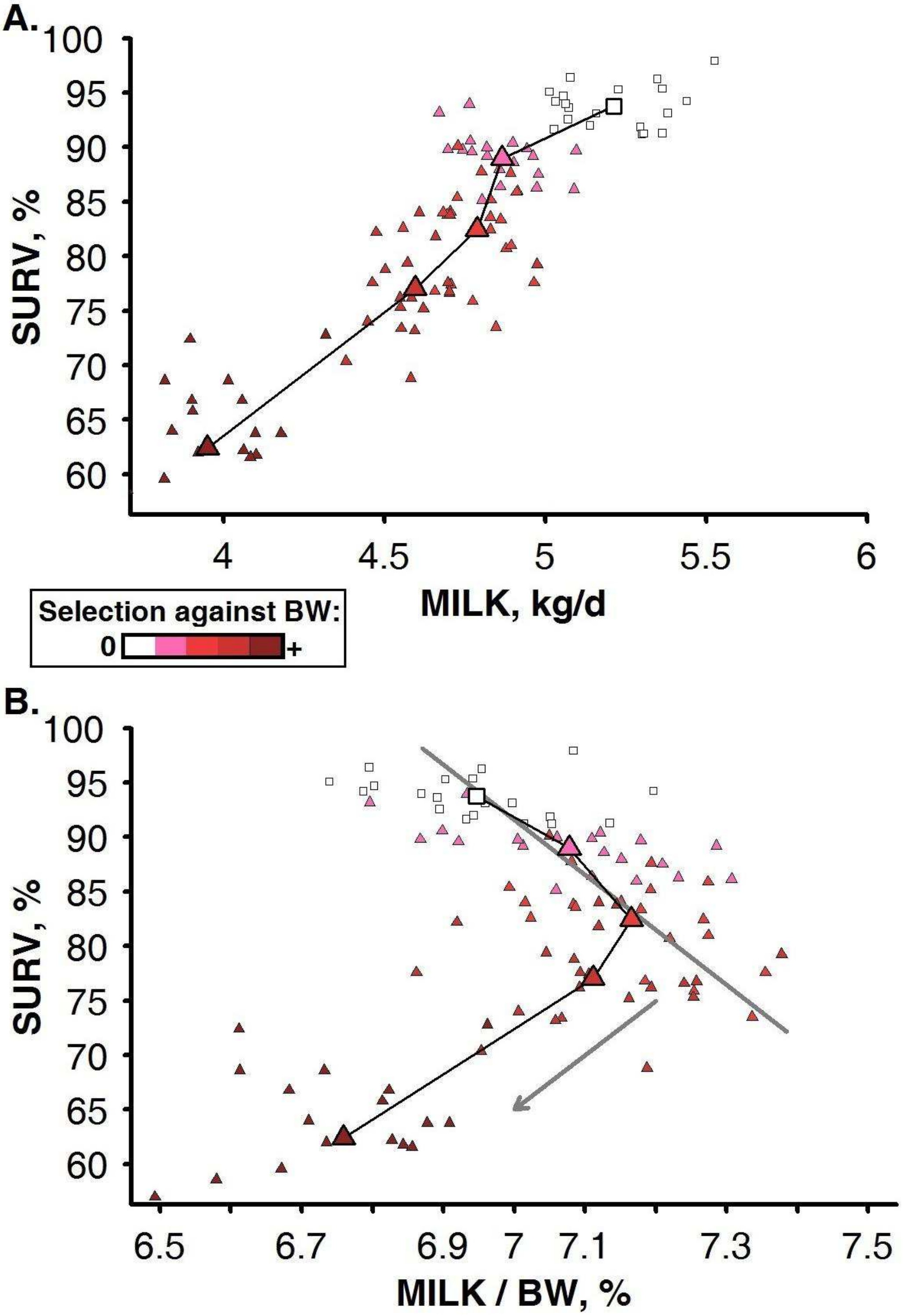

Figure 3-4 : Relationships between the herd survival rate (SURV) and milk production, estimated as the average peak milk yield (MILK) alone (A) or relatively to the average body weight (MILK / BW) (B), when selecting for milk yield alone (white square; i.e. S_Y strategy) or combined with different weightings against BW (-0.5, -0.75, -0.85, -1 with increasing density of shading) in a abundant and constant environment. Selection was practiced during 40 years of selection and the average of last year (big symbols) is shown for each strategy with its 20 replicates (small symbols).

An increase in l_0 was almost linearly related to an increasing penalty imposed on BW. Initially, the increase in l_0 had a moderated effect on SURV (Figure 3-5). In addition, increased values of l_0 due to the selection for milk production efficiency were not associated with a reallocation of energy from body reserves to the subsequent allocations in the hierarchy. If this had been the case, it would lead to large animals because before the first reproduction the energy reallocated from body reserves (i.e. a decrease in d_0) would be towards growth and survival. When BW was increasingly selected against, such a decrease in d_0 (compared to its initial value at the beginning of selection ≈ 0.25, Figure 3-2) was less and less selected for. Beyond an average value of l_0 (≈ 0.86) the resource allocated to survival became so low that SURV decreased dramatically (as a consequence of the sigmoid function used to describe the survival likelihood).

The above trade-off might result from the assumption of an absence of genetic variation at the level of the resource allocation between growth and survival (g_0). If this variation would exist, one could hypothesize that a decrease in g_0 would allow for a reallocation of the resource from BW to survival when selecting against BW. This was not explored in depth and was thus not reported. However, it appeared that the negative effect on survival was reduced compared to the present results but still considerable (SURV ≈ 80% with $W_{BW}= -1$). In this case, an alternative hypothesis would be that the trade-off observed in Figure 3-4B still exists but takes a different shape (e.g. convex). This would deserve a deeper exploration.

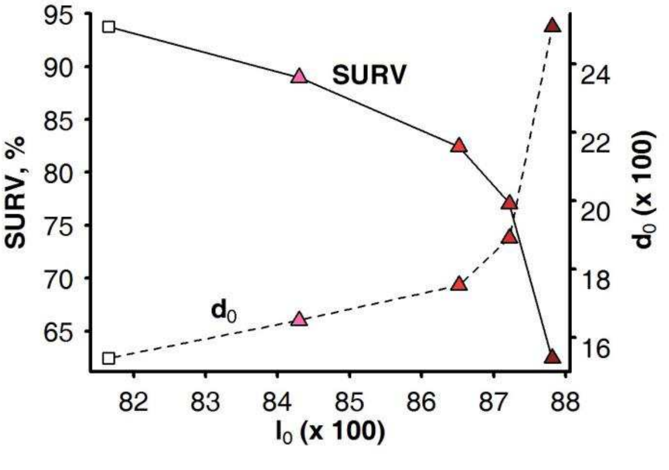

Figure 3-5 : Relationship between the average value of heritable trait of resource allocation for lactation (l_0) and that of body reserve deposition (d_0, dotted line) and the herd survival rate (SURV, continuous line) in a abundant and constant environment. The l_0 increase results from an increasing penalty on BW (0, -0.5, -0.75, -0.85, -1 with increasing density of shading as used in Figure 3-4) in addition to selection for milk yield. Selection was practiced during 40 years of selection and mean values (20 replicates) are from the last year for each strategy.

2 Description of extended lactation (EL)

Our experimental study on EL provided evidence that a key effect of EL is to disrupt the phase opposition between MY and BW dynamics which usually takes place during a normal lactation (Figure 3-6). This effect appeared to be primarily driven at the onset of EL by a predetermined increase in resource acquisition (probably triggered by a seasonal cue), and was then characterized by a delayed transfer of energy from feed to milk. The individual variability observed in the relationships between milk production, live weight and intake at the onset of EL suggested that suitability of goats for EL is mostly based on a tendency for partitioning energy towards milk production instead of to body tissue gain during the onset of EL and possibly on a high NL persistency. However, there was not enough data to make a consistent assumption.

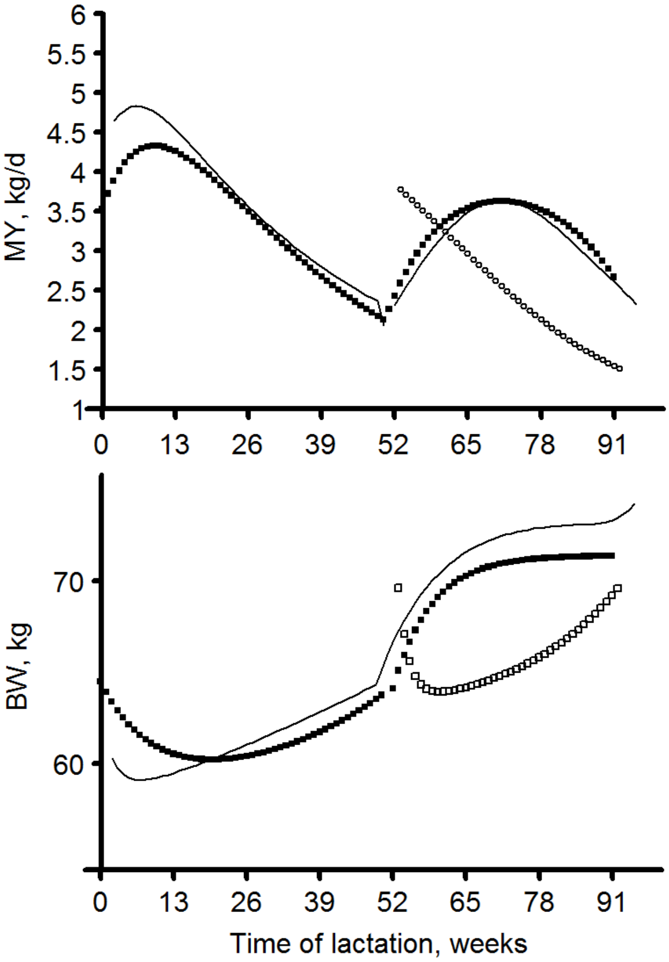

Figure 3-6 : Time-profiles of milk yield (MY) and body weight (BW) for dairy goats undergoing extended lactation (black square). One year after kidding (at week 0), MY and BW increased. At this moment, MY and BW of goats that had a new parturition are indicated (white square). Data were smoothed values obtained from Douhard et al. (2013). Continuous lines indicate the fitted values of the model (obtained with $l_0 = 0.8$ and $d_0 = 0.22$).

Based on our characterization of EL, two main new features were included in the model: 1) a transient increase in resource acquisition assumed to be triggered by a seasonal cue at about 330 days in milk, and 2) an increase in resource allocation towards body reserves deposition (d) and towards lactation (l) occurring almost simultaneously with the change in acquisition. These features were roughly parameterized using the EL data of our study (Figure 3-6, continuous line).

3 Exploration of selection strategies allowing for the use of EL in a variable environment

In the V-environment, our results showed that selecting for longevity in addition to milk production, was consistently reflected in the survival rate (SURV): the greater W_{AGE} in the SelIndex, the greater SURV simulated. However, the selection response for MILK and BCS was quadratic. When animals started to be selected not only for their high milk ($W_{MILK} = 1$) and fertility ($W_{PREG} = 1$) but for their age as well, MILK was decreased and BCS increased. However, above a value of W_{AGE} (between 0.10 and 0.25), the direction changed; MILK increased and BCS decreased. This change of direction in the response to selection for age was due to a correlated increase in the proportion of EL in the herd. There was a value of W_{AGE} (between 0.10 and 0.25) above which the importance given to age in SelIndex is so high that older animals become systematically preferred regardless of their reproductive status. This had the effect of dramatically increasing the proportion of EL.

When selection for longevity was associated with high proportions of EL, the biological features of EL assumed in the model (Figure 3-6) changed the selection pressure on the heritable traits of resource allocation (Figure 3-7). Females that underwent EL had no genetically driven mobilization of their body reserves when a new rise in milk yield occurred and had more time to recover body reserves from their previous parturition. This allowed them to survive and reproduce successfully latter, during the EL phase. Consequently, with high proportion of EL, the pressure to maintain high values of body reserves deposition (d_0) was relaxed and could even decrease (as reflected in BCS). Moreover, as selection for age did put pressure for a greater allocation to lactation, the resource driven away from body reserves was thus mainly reallocated to growth and survival instead of to lactation. The increase in body size led to a greater desired intake (R_G) so that finally MILK increased.

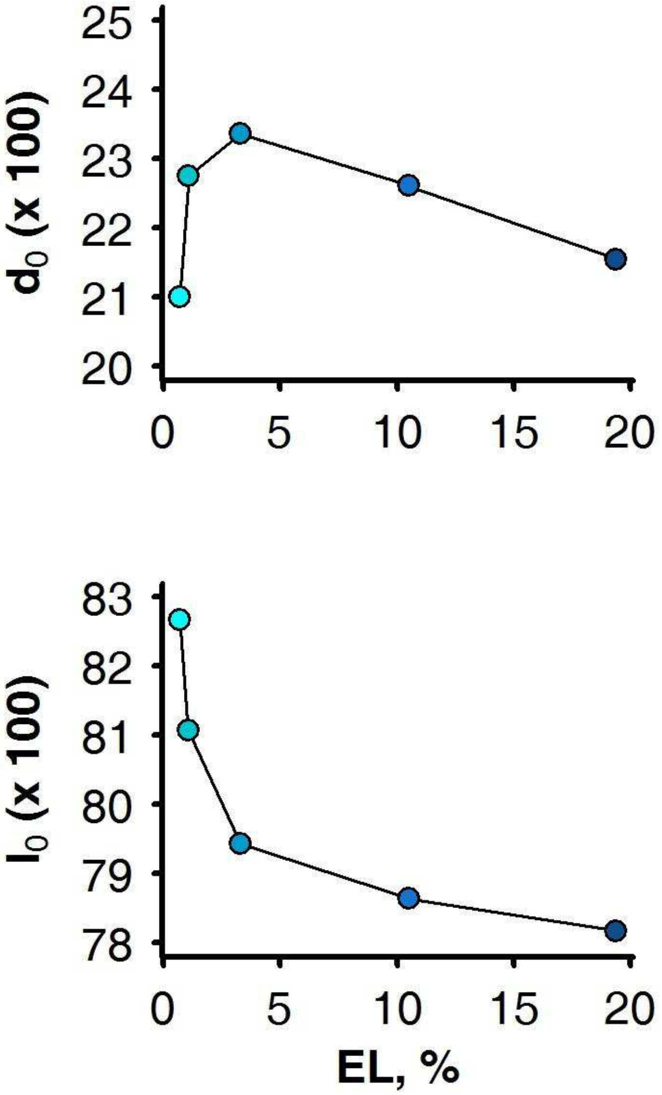

Figure 3-7: Relationship between the proportions of extended lactation in the herd (EL) and the average value of heritable traits of resource allocation for body reserves deposition (d_0) and for lactation (l_0) obtained after 40 years of selection for milk yield and a different emphasis on age (increasing density of shading of the points) in a variable environment (V environment for scenario definition). Values are the means of the last five years of selection (20 replicates).

The net effect of combining selection for age with EL is reported in Figure 3-8. The top panel shows that as long as the proportion of EL remained low (circles), putting more emphasis on age improved survival but this was achieved by a trade-off with milk yield (grey lines) because the limited quantity of resource obtained was driven away from lactation towards body reserves. Further selection for age increased the proportion of EL (squares) and this allowed the trade-off between MILK and survival (arrow) to be alleviated (i.e. a ‘win-no loss’ situation). By modulating the consequences of reproductive failure, EL relaxed the pressure to maintain a high resource allocation to body reserves that was needed to remain in the herd. The bottom panel shows however that the positive effect of EL was not so apparent in terms of milk production efficiency, here approximated with the ratio between MILK and BW. Even if MILK was increased, the females selected were indeed bigger and tended to gain fat during EL.

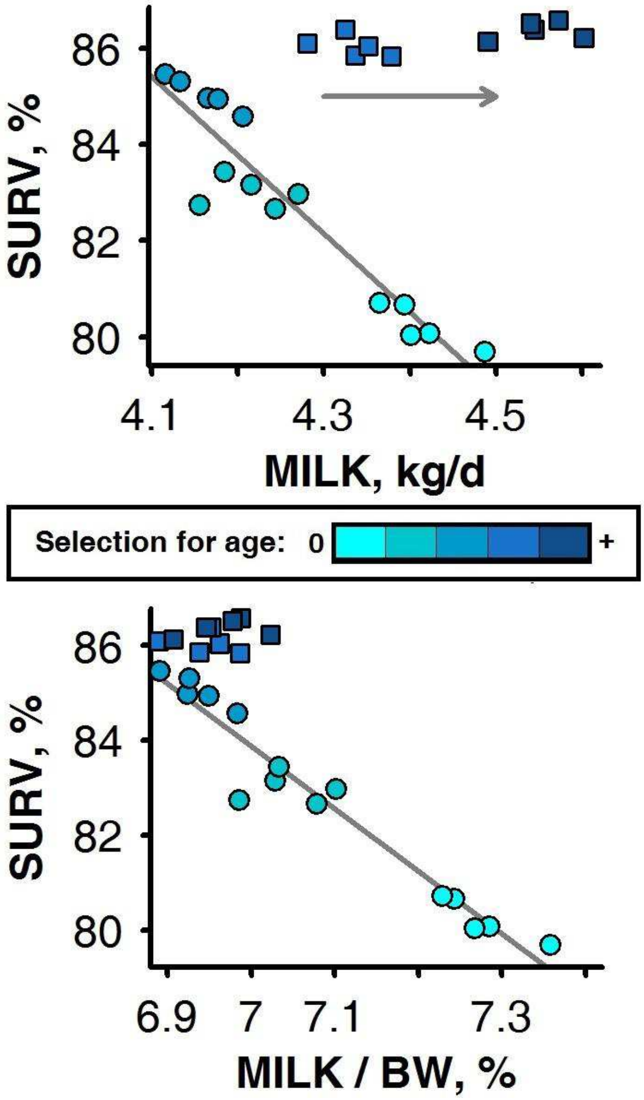

Figure 3-8 : Relationships between the herd survival rate (SURV) and milk production, estimated as the average peak milk yield (MILK) alone or relatively to the average body weight (MILK / BW), when selecting for milk yield combined with an increasing emphasis for age in a variable environment. High selection for age resulted in a high proportion of extended lactation (squares) compared to the others strategies (circles). Selection was practised during 40 years of selection and the last 5 years (20 replicates) are shown for each strategy.

Chapter 4: DISCUSSION

Three aspects of the Ph.D. are successively discussed in this chapter. The first aspect addresses the biological meaning of the Ph.D. results (Figure 4-1, (1)). We then step back to the framework to show the limits of using the animal description proposed as input (Figure 4-1, (2)). The methodological contribution of the approach and the potential for further generalization are highlighted. Finally, the Ph.D. contribution is addressed in the context of the design of sustainable management systems (Figure 4-1, (3)). A step forward is indicated with a new approach for iteration.

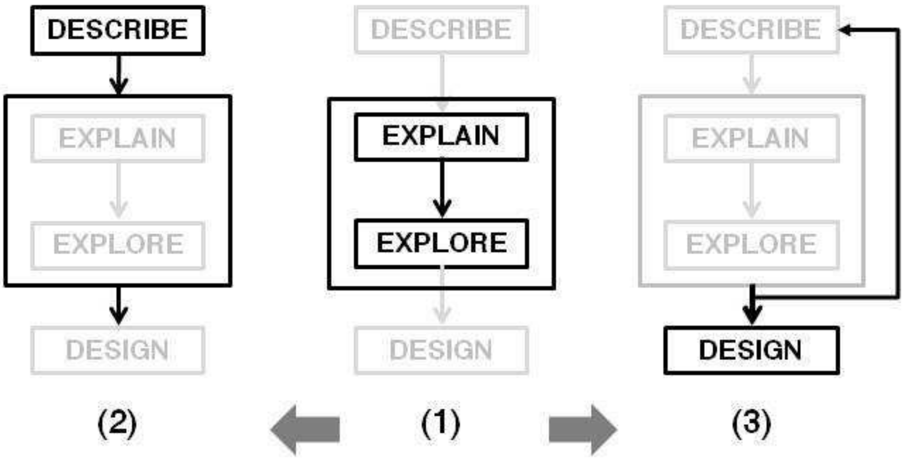

Figure 4-1: Three aspects of the Ph.D. highlighted by the research approach: (1) a biological explanation of the genotype-environment interactions that enables the exploration of different scenarios of production and selection at the herd level, (2) a framework that uses a set of assumptions from resource allocation theory as inputs to describe an animal model in the herd context and (3) a step towards the design of sustainable management systems and for a new research approach iteration.

1 An application of the resource allocation approach to the herd context

1.1 Outcomes from the resource allocation approach

An application of the resource allocation theory to the context of farm animals is not straightforward because contrarily to natural environments; (1) selection of the genotypes is redirected from natural fitness to the manager's priorities, and (2) the herd environment in which animals perform is controlled such that the manager's priorities can be satisfied.

A first interest of considering (1) based on a resource allocation model is to highlight unexpected changes in the genetic relationships which may arise during selective breeding (Van Der Waaij, 2004). This may benefit animal breeders by allowing them to foresee the constraints to long-term selection in the hierarchical breeding scheme (Bijma, 2009). However, it provides few insights on opportunities for, and constraints to, managing G × E in alternative ways to that of solely focusing on selection. Our application of the resource allocation theory is, to our knowledge, the first attempt to do so at the level of individuals within a herd. Opportunities and constraints were highlighted by exploring some of the combined effects of (1) and (2) (Figure 4-2).

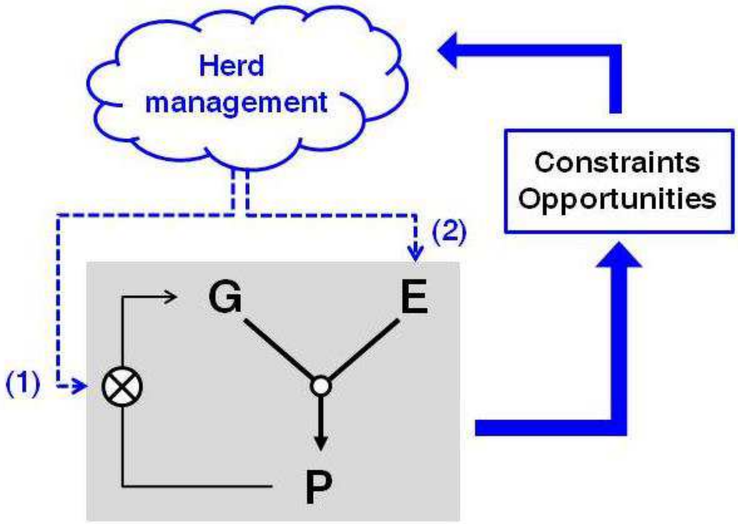

Figure 4-2 : Contribution of the Ph.D. for identifying opportunities and constraints to exploit genotype-by-environment interactions within the herd. This was done by exploring some of the combined effects of selection (1) and management (2)

Long-term simulation results provided in Chapter 3: illustrated complex interactions between the production and selection processes when they were practiced together in the same herd environment. Overall, the local herd environment tailored different allocation priorities throughout generations. The expression of these resource allocation priorities, in turn, shaped the form of the relationships between traits obtained over the long-term:

i. In a controlled and abundant environment, selection for milk production did not impair the survival probability as long as the development of intake capacity through generations could keep pace with the progress in milk production. This condition was however compromised when the selection objective was redirected towards short term production efficiency (i.e. high milk yield combined with low feed costs) and a trade-off between milk production efficiency and survival emerged (Chapter 3:1).

ii. In an uncontrolled and variable environment, it was not possible to increase milk production without decreasing the chance of survival, unless the management priority on the succession of the reproductive cycles was lowered such as the proportion of EL could increase (Chapter 3:3).

In both cases, selective breeding within the herd was thus constrained by a trade-off between survival and milk production (ii) or its efficiency (i). Selection for any one of these production components put the greatest pressure on the most limiting trait of resource allocation (i.e. for lactation, l_0) and ultimately affected survival, as was the case in the model of Van Der Waaij (2004). However, the present results also indicate that an adjustment in the degree of management priorities (e.g. the control of reproductive failure) may change the direction of selection and alleviate the trade-off (i.e. a win-no loss situation).

From a biological viewpoint, our approach stresses the importance of nutritional effects on selection responses. Clearly, others types of constraints not considered in this thesis may be involved in trade-off emergence (e.g. phylogenetic, genetic linkage; Stearns, 1992; Zera and Harshman, 2001). The above results focused on functional constraints to selection. They illuminate the potential significance of key physiological mechanisms expressed during animal lifetime; 1) the desired resource intake, 2) the conservative strategy relying on body reserves and 3) the tactical approach to cope with the cost of reproduction. Most of these mechanisms were already integrated through the initial model assumptions on animal physiology, which inevitably leads to some circularity. However the multi-scale approach brings a new dimension to the analysis; the simulation outputs at the herd level provide an estimate of the potential significance of the physiological mechanisms assumed at the animal level in different selection contexts. This is discussed in the following sections.

1.2 The desired resource intake

In an abundant nutritional environment, an increase of resource acquisition capacity throughout generations seemed a necessary condition to increase milk production without impairing survival. This was determined by state-based relationships central to the model; intake was positively related to the body size (non-labile body weight) and negatively with body fatness (Tolkamp et al., 2006). Based on these assumptions, selection for milk yield resulted in a systematic correlated selection against body reserves. Females lowered the priority to deposit fat to increase their intake and take a greater advantage of their safe nutritional environment. In these conditions, the decrease in body fatness was a cause of the increase in intake through generations selected for high milk yield, whereas it is usually considered as a consequence of intake not keeping up with genetic progress in milk yield (Veerkamp et al., 2003; Dillon et al., 2006). This raises at least two questions: is it really advantageous to be larger and leaner in a safe environment? And, what is limiting the progress in intake in these conditions?

For the high yielding dairy cow selected in a favourable environment, an increase in body size is supported by observations of a positive genetic correlation between milk yield and growth (Mantysaari et al., 2002; Coffey et al., 2006). However, there is little evidence indicating that greater body size benefits survival in farm animals. Growth parameters have in some cases been found to be negatively associated with health traits (Brotherstone et al., 2007). However, there are likely different directional forces operating. Animals that prioritise growth over survival will be big and unhealthy. However, animals that are unhealthy will not grow as well. Hence the relationship between growth and health might be expected to flip depending on the healthfulness of the environment (Doeschl-Wilson et al., 2009). In our model, a great size was not an advantage when the resource availability was decreased (Paper 1). Due to their high and fixed cost of maintenance, big and lean females suffered greater mortality under resource shortage. This fits with evidences of large dairy cows highly selected for milk which are healthy as long as they are fed a nutrient-rich diet but suffer greater problems than smaller cows (with equivalent genetic merit) in a more limiting environment (Kolver et al., 2002). In harsh environments, a small size is deemed to be advantageous, not only because of a low absolute metabolic rate, but also because of a superior grazing ability (Illius and Gordon, 1987; Provenza, 2008). As a whole, the above evidences suggest that being larger and leaner is thus advantageous only if the environment is safe (i.e. a high and constant resource availability). In these conditions, our model predictions fit with expectations from the resource allocation theory (Beilharz et al., 1993) and our initial expectations (Chapter 1:3.1). However, similar conditions also suggest that a limit to the increase of intake may exist and lead to different outcomes. In this context, the question of what is limiting intake seems of paramount importance, in particular to better understand the reason of a decrease in body fatness.

In an abundant nutritional environment, our results implied that during selection for milk production, body size was the limiting factor to energy intake as selection against live weight impaired survival. In selection experiments in mice (Rauw et al., 1999) or in rabbits (Savietto et al., 2013), live weight and intake generally increase when one reproductive trait (e.g. litter size) is selected for. However, even without a selection penalty on live weight or intake, the correlated increase seems limited and ultimately generates a trade-off between the trait selected for and another trait (e.g. litter survival). This suggests that some process was limiting intake and increased the selection pressure for a reallocation of energy towards the trait of interest.

In our model, the control of the desired intake was described at a high level based on the lipostatic theory (Kennedy, 1953) and its consideration in ruminants (Faverdin et al., 1999; Stubbs and Tolkamp, 2006). However, a more common assumption is that intake of the dairy female is actually limited by the (genetic) potential of the mammary gland. In mice, this has been supported experimentally (Hammond et al., 1996) but then challenged by a series of contradicting findings (reviewed by Speakman and Król, 2011). Our experiment in well-fed dairy goats undergoing EL indicated that a markedly increase in intake occurred a long time after parturition and was apparently not driven at the level of the mammary gland (Paper 2). Moreover, intake was increasing simultaneously with live weight which was apparently not congruent with a lipostatic control. Among the others hypothetic processes, an interesting one in the context of genetic selection of ruminants is that intake is actually limited by the body capacity to dissipate heat (heat dissipation limit theory, Speakman and Król, 2010). Heat stress is indeed one factor identified as potentially limiting intake in the dairy cow highly selected for milk yield (Kadzere et al., 2002). I might also be congruent with the innate increase of intake we observed during EL if we consider this as an evolutionary adaption of the dairy goat to the seasonal temperature variation (Linzell, 1973; Rhind et al., 2002). Undoubtedly, considerations from both experimental and evolutionary biology would benefit to the issue of what is limiting intake.

1.3 Environmental variability reveals the evolutionary importance of body reserves

A decrease in body fatness and fertility due to selection for milk in an abundant environment is well supported by observations in the high-yielding dairy cow (e.g. Coffey et al., 2004). However, this decrease is in reality probably not as sharp as suggested by the model presented in this thesis. This might be due to an overestimation of the feedback between the body fatness and the desired resource intake. Another explanation is that others biological mechanisms are negatively impacted by low body fatness. Indeed, body reserves have multiple and complex associations with other performances (Roche et al., 2009). For instance, lean animals could be more at risk to pathogen infections possibly, in part, as an effect of greater exposure to cold stress. Overall, the decrease in fatness simulated in our model suggests that in a nearly perfect environment, free from these effects on survival, body reserves have no evolutionary importance. This ideal environment obviously does not exist although it might be approximated in highly controlled intensive livestock systems.

In a variable environment, our simulations show that body fatness was maintained even if it was not actively selected for by the manager (Paper 3). Further, greater levels of body fatness were observed when selection for longevity was included in the breeding objective and a high management priority was placed on achieving genetic progress in reproductive success. Thereby, survival could be improved but it came at the cost of reduced milk production (Chapter

3:3). This emphasizes the animal's priority to maintain body reserves which is central in the life history strategy of long-lived mammals (Sæther, 1997; Gaillard and Yoccoz, 2003; Hamel et al., 2010a). In natural environments with wide variations in resource availability, animals develop conservative strategies that prioritize longevity as the first means to maximize fitness. For instance, after parturition in spring, bighorn ewes tend to decrease their lactation effort for the current offspring if the resource availability is decreased (Martin and Festa-Bianchet, 2010). Thereby, they seem to target a level of body reserves that maintain their chance to survive later during winter when resource availability is scarce. Because of this conservative strategy, costs of reproduction (i.e. gestation and lactation) on maternal survival are rarely found in the wild (Hamel et al., 2010). Using a resource allocation perspective, these authors suggested that survival traits of long-lived species have probably been canalized during thousands of years of natural selection. However, there is probably still some little genetic variation and it might be hypothesized that selective breeding has actually used it because most emphasis has been placed on others traits competing with survival (e.g. lactation). To some extent, such hypothesis was thus confirmed by our model because i) selecting solely for milk impaired survival when the resource availability was limited, ii) in this situation, putting more emphasis on age improved survival and favoured animals with a high priority to deposit body reserves and iii) this priority was depreciated when selection was practiced in a favourable environment. Under this hypothesis, a ‘balanced’ selection index that combines milk production with age and body condition score seems highly desirable.

1.4 Extended lactation as an animal tactic to deal with the cost of reproduction

So far, the relation between body reserves and fertility has not been discussed here. Though, this is the most obvious negative side-effect of selection for high milk production (Rauw et al., 1998). In our model, the probability to conceive was assumed to be directly related to the level of body fatness and the rate of body reserves deposition (Friggens and Chagunda, 2005). Considerable evidences for wild animals also support this assumption. Choosing to reproduce at one moment of the year may have negative consequence for future survival during periods of high energy expenditure (late gestation and early lactation). Relying on body reserves to decide on reproduction seems thus a tactic in adequacy with the survival priority of long-lived mammal (Bårdsen et al., 2011). If such risk-adverse tactic have also been encoded in the genetic make-up, it might be not so surprising to see that the system “acquisition - body reserves - fertility” was relatively maladapted (especially in terms of fertility) to an abundant and safe environment (Stubbs and Tolkamp, 2006).

In long-lived mammals, a cost of reproduction on maternal survival is rarely found, however, considerable evidences demonstrate a cost of current reproduction (i.e. lactation) on future reproduction (i.e. subsequent lactation or conception) (Hamel et al., 2010). Our characterization of EL (Paper 2) also suggests that during their natural evolution goats have developed mechanisms to compensate for a low fertility post partum (as reproduction is also a major component of fitness). The simultaneous increase observed in milk yield and live weight could benefit respectively the current offspring (which is suckling) and the mother's probability to successfully conceive when she is giving another opportunity to do so. Our results also suggest that the relative priority for these two functions vary importantly between individuals. If a genetic basis for the traits controlling EL exists, there might be more variation than for the regulation of the resource allocation post partum. This could be due to the fact that EL has been relatively rare during evolution so that selection pressure for the underlying traits has also been relatively low. Such variation could be of interest for selection.

From a physiological viewpoint, the effects observed during EL (Paper 2) seem to be driven by regulations of feed intake and tissue metabolism specific to seasonal breeders. In particular, it has been shown that long day length increased adipose tissue leptin expression and lipogenic activities, and decreased lipid mobilization, in non-productive ovariectomized, pair-fed ewes (Chilliard et al., 1998). Thus season per se could have teleophoretic effects on body tissue metabolism independently of feed intake regulation (Chilliard and Bocquier, 2000). However, these effects normally occur with increasing photoperiod whereas the effects observed in our experiment were in early winter when day length decreases. In bucks, it has been suggested that changes in tissue metabolism can be driven by programmed changes in feed intake regulation across seasons, occurring independently of the food availability (Walkden-Brown et al., 1994). Moreover, lactating cows and goats are hypoleptinemic, including during late lactation and/or when in positive energy balance (thus probably also during EL) (Chilliard et al., 2005), which could favour both appetite and energetic efficiency in combination with the effect of body fatness. Therefore, it is likely that EL is regulated by complex interactions between different metabolisms (from fat tissues and from the mammary gland) to reduce energy expenditure and increase intake according to seasonal cues. Leptin, and especially hypoleptinemia probably plays a central role in these regulations.

1.5 Implications for the management of G × E: from constraints to opportunities

The simulation outcomes discussed above (sections 1.1 to 1.4) converge to a consistent conclusion that the most likely opportunities to manage G × E and exploit the biological capacities, such as EL, are in variable production environments. This also converge towards recent incentives for the incorporation of ecological consideration into livestock system research (Provenza, 2008; Bocquier and Gonza, 2010; Hackmann and Spain, 2010; Dumont et al., 2013).

In intensive situations, the constant provision of a nutrient-rich environment generally requires a high management priority to control the high feed costs, i.e. efficient animals are needed. Selection against mature body weight has been proposed as a way to improve short-term efficiency (Veerkamp, 1998) and is already part of the strategy used in many breeding programs (Miglior et al., 2005). From a herd perspective, we suggest that this will ultimately contribute to increased health problems (Chapter 3:1.2), unless the improvement of the managed environment (e.g. higher food quality) keeps up with the genetic trend for milk yield. Such conditions will probably be more difficult to achieve in the future. In this context, the benefits of increased short term efficiency might be overwhelmed by increased health and replacement costs (Benoit et al., 2009). A crucial challenge seems thus to be to redirect the approach of selection from short-term to long-term efficiency.

Our studies indicate that opportunities to do so at the herd level exist both at the level of nutrition and selection. In a less controlled nutritional environment, animal priority to maintain body reserves was naturally favoured. Moreover, selecting for longevity was acting in concert with the conservative strategy of long-lived mammals. In controlled herd environments, the design of nutritional strategies with a variable provision of feed throughout the year –so as to take advantage of the body reserves dynamic– seems a promising avenue that is already being explored (André et al., 2010, 2011). Such solutions fit well with the overall challenge of reducing inputs and their negative environmental impact, in intensive systems (Dumont et al., 2013).

In this context pasture-based and pastoral systems seem favoured. We showed a synergy between a ‘balanced’ selection for milk and longevity and using some proportion of ELs in the herd. Thereby, high-producing females could be kept longer within the herd. Even if these goats were less efficient during their EL, this might be acceptable in a pasture-based system as an high grass intake is economically desired. In spite of crucial physiological differences between the dairy cow and goat reproduction, these results are consistent with previous findings in the dairy cow in pasture-based system (Kolver et al., 2007) suggesting that EL is a particularly suitable for high-yielding genotypes. Integrating the specific nutritional mechanisms in the management of seasonal breeders like the dairy goat may open promising perspective for the design of innovative systems. In particular, this may open up possibilities to manage individual variability based on G × E knowledge; for instance combining specialist genotypes managed for EL with more generalist genotypes able to successfully reproduce every year to ensure replacement within the herd. This would allow assessing the insurance function of a management system that is already practiced but with different species (Tichit et al., 2004) but not in mono-specific situation.

In situations of uncertain feed supply, the biological benefits of body fatness in terms of health and reproduction have to be balanced with the economic costs of excessive fat deposition (Young et al., 2011). For instance in pasture-based sheep production systems a research interest is to find the optimal live weight profile based on both nutritional (Thompson et al., 2011) and genetic (Rose et al., 2013) solutions. Obviously, this requires a methodology to successfully integrate these two aspects and we expect our model to contribute to this effort.

2 The framework

2.1 The emergence of G × E interactions at the herd level

A key contribution of this thesis is to the development of methodology that allows for the exploitation of G × E (Knap and Su, 2008). In the view we proposed, G × E is not considered as a result per se but rather as a multi-level dynamic process that involves the farm manager. It differs from the traditional approach of G × E with reaction norms (usually expressed as a plot of phenotypic values against environmental values (Simm, 1998)). In this latter view, the term 'interaction' is used when the slopes of the reaction norms are different for different genotypes without making explicit the underlying mechanisms through which G acts on E and vice-versa (Lewontin, 1974), especially within animal lifetime (Friggens and Newbold, 2007). Thereby, opportunities to manage G × E using reaction norms are limited to the selection of genotypes over generations, provided that sufficient data is available to estimate the genetic parameters of the reaction norm (Kolmodin et al., 2002; Bryant et al., 2006), i.e. when the selection process is organized at a larger scale than the herd production process. When herds do not belong to a hierarchical organization of genetic improvement or when germplasm should come from within the management system in which it is to be used (Dillon et al., 2006), the view we propose might be valuable as it sheds light on the perspective to manage G × E by herd management itself.

Hierarchical selection is usually practiced in a favourable and highly controlled environment to subsequently transfer the improved genotypes to the production environments with variable conditions. The selection process and the production processes are thus approached separately (Figure 4-3a). By contrast, the approach considered in this thesis is to conceptually integrate the selection and the production processes within the same local herd environment (Figure 4-3b).

This implies that both the influence of the selected genotypes on the production response and in turn, the influence of the performance on the selection process is represented. Thereby, the animal responses to their nutritional environment take place in a herd selection context, i.e. they are obtained from genotypes selected according to prior performance in the local environment (Figure 4-3b, arrow downward). These phenotypic responses (including animal 'survival), in turn, shape the responses to selection, i.e. the genotypes for the future, according to the performance criteria defined by the manager (Figure 4-3b, arrow upward).

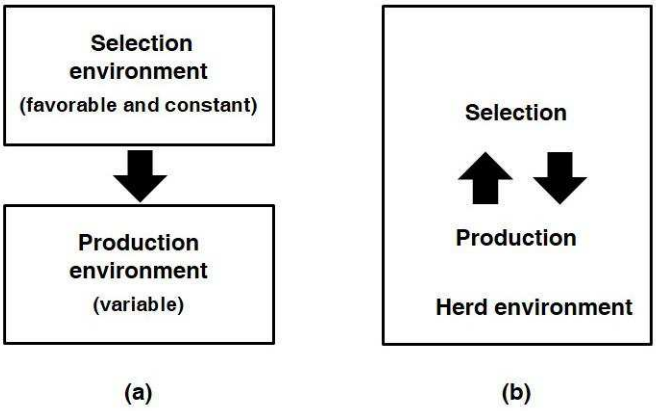

Figure 4-3 : Two simplified views on the association between the selection and the production processes with the environment in which they are practiced

2.2 Management influences in the local herd environment

Not only does the developed model show that selection under local conditions (i.e. in the same herd) is a quite different situation than that in hierarchical selection schemes, it also shows that both the selection strategy and the management strategy will alter the genetic make-up of the herd over time, in ways that are not always easy to predict without simulation.

Non-linear abrupt changes in the response to selection emerged from our model simulations as a result of different management priorities. In one case, it indicated when too much priority on milk production efficiency has a catastrophic influence on survival (Figure 3-4). In the other case, it indicated when a diminishing priority on reproductive success allowed for a 'win-no-loss' production improvement (Figure 3-8). This suggested some threshold of unitary milk production (kg of milk per kg of live weight) where management becomes highly risky for survival. There also seemed to be a threshold for the proportion of ELs in the herd, above which it became an effective lever to maintain herd performance and robustness.

The identification of management thresholds seems rarely done in the context of animal production in developed countries although this would be desired (Darnhofer et al., 2010). One reason might be that catastrophic changes such as the extremely high rate of mortality simulated in the model are rarely observed in practice. High losses are rather observed under harsh conditions such as drought in pastoral systems where the whole system can collapse. In this case, the identification of threshold can be used to shed light on the conditions of effective insurance practices such as herd diversification against unpredictable climatic events (Tichit et al., 2004). Though, as catastrophic changes emerged abruptly in the present simulations, it seems valuable to investigate their probability in systems where collapse is actually unexpected. This probability will increase as the global context of the farm becomes more variable and uncertain. In this case, variations in the global farm environment may overwhelm the local herd environment even if it tightly controlled by the manager (see for instance the dramatic rate of mortality in broiler chicken farms subject to heat stress). This emphasises another interest of threshold identification which is promoting an adaptive herd management. In our case, it would be interesting to develop a methodology to investigate which tactical adjustments in management would aid the maintenance of different long-term selection objectives in a challenging global farm environment.

2.3 Distinguish the selection practice from the selection action

A key feature of the model was to distinguish the observable traits on which selection is practiced, from the traits on which selection is acting, i.e. the resource allocation coefficient (c). Heritability was set at the level of nutrient partitioning traits underlying the performance. Choosing the level of the resource allocation allowed for the notion of trade-off between functions to be placed at the centre of the approach (Friggens and Newbold, 2007), and to explore the conditions of its emergence at the herd level. This approach fits well with the increasing number of mechanistic models of nutrient partitioning that have been developed over recent years (reviewed in Friggens et al., 2013). Even if these models have seldom incorporated a heritable component (Bryant et al., 2005), they may provide a useful basis to further explore genetic components of nutrient partition, i.e. with parameters others than “c”. A pertinent issue in this context relates to the fact that all of the current nutritional models rely on the notion of a genetic potential of performance level per se combined with the so-called “requirements approach” to determine intake (Emmans and Kyriazakis, 2001). To our knowledge no animal model using the requirements approach with short time-steps has been integrated yet into a population/herd structure so as to test responses to selection. We thought that setting heritability at the level of the resource allocation was a consistent assumption based on an explicit evolutionary principle, and supported by a lot of modeling studies in population genetics. Developing a similar approach using the classic requirements approach by setting heritability at the level of performance per se would be an interesting way to compare the long-term value of these two different approaches.

Because we did not have the time to create formal validation data, the modeling approach used in this thesis was developed as a proof-to-principles, and thus the first results only demonstrate its feasibility. To turn this approach towards more realistic situations and enable a more predictive application, it would be necessary first to develop an appropriate methodology to facilitate a connection with real data. A key question in particular is how to estimate the genetic variability in allocation coefficients (c) that describe genotypes from these real data? Before coming to this perspective, we first address the actual limitations of the model.

2.4 Model limitations and evaluation

- ***Limitations***

The model developed in this thesis was primarily intended to link the selection process to the animal production process within a herd. Most emphasis has been placed on representing the interaction between the two processes; as a consequence each process had a high level of description. This has imposed some model limitations.

With regard to selection,

- The selection index did not use pedigree information on relatives to estimate breeding values for the traits (except for replacement which was chosen according to their mother score of the prevailing year). This could be improved by considering information on previous years (i.e. repeated record), as well as those of others relatives (e.g. half sibs), although this moves away from common on-farm practice. Moreover, the selection index was also crude in terms of the way it applied weighting to alternative traits. Usually weighting of traits depends on economic values and frequency of expression whereas it was not considered here. This is based on a well-developed methodology which can even incorporate ecological, social and ethical priorities providing that it could be valued in the breeding objective (Olesen et al., 2000).
- Progeny testing was not considered to select males. If males were selected based on performance of their offspring this might increase the efficiency of selection. Such a process could be required if part of the males gametes were considered to be imported into the herd (e.g. use of artificial selection). In goat production systems, this is however quite limited compared to dairy cow systems (Leboeuf et al., 2008).
- Mating was assumed to be random whereas in practice, the farm manager may select the pairs that reproduce together (although reproduction is generally managed at the group

level in the dairy goat). Another purpose of non-random mating is for the control of inbreeding which may cause problems.

With regard to production:

- A narrow description of the animal environment was considered. With regard to nutritional factors, the resource was only described in terms of metabolizable energy. If, for instance, other nutrients were limiting then energy allocation should not actually trade-off (Stearns, 1992). Moreover, non-nutritional factors that are usually controlled during selection of elite breeders (e.g. temperature or pathogen load) may stress the importance of particular trade-offs such as disease resistance vs. growth (e.g. Doeschl-Wilson et al., 2009).
- The desired resource intake accounted for the notion of intake capacity relative to a filling effect of the diet as it was defined as a function of body size. However, this was crude compared to the representation in actual feed systems (Sauvant et al., 2007) and may need to be refined, especially if variations in the resource quality (especially forage) were to be simulated. In the model, the effects of environmental limitations were considered to apply, in general terms, to resource availability. As such, the specific situation where it was resource quality rather than availability that was limiting, i.e. resource intake was limited by the physical properties of the feed, was not explicitly considered. It would probably be of value to explore the difference between these two modes of restriction of intake to see to what extent they impact different parts of the herd population, as this would ultimately affect performance of these animals. Nevertheless, it should be noted that feed quality limits occur far less frequently for ruminants compared to mono-gastric farm animals such as pigs (Hackmann and Spain, 2010). A deeper representation of resource acquisition features typical to ruminant nutrition (e.g. feed interactions forage/concentrate, foraging behavior) seems relevant as the role of resource acquisition on trade-offs emergence take precedence on the role of allocation. The present model suggests however that integrating the acquisition and allocation effects is a fundamental issue when applying the resource allocation theory to farm animals.
- Management was not adjusted during simulations. The mating calendars, the rate of voluntary culling and herd size were constant. If, for instance, the reproduction failures could be compensated for by having another mating period during the year, probably EL would not be as influential as suggested in the model. Representing different reproductive periods through the year would however require accounting for the reproductive seasonality, which is a key aspect in seasonal breeder such as the dairy goat (Leboeuf et al., 2008).

- ***Evaluation***

In addition to the above model limitations, a thorough evaluation of the model would be desired. It is however complicated by the different levels of parameters, i) the genetic parameters of the heritable traits (phenotypic population mean and standard deviation, heritability) which directly influence the selection response, ii) the survival and conception likelihood parameters which influence the herd demography independently from the manager's control, and iii) the resource acquisition parameters which determine the strength of the feedback between allocation (through body weight and the body reserves) and acquisition.

Moreover, any sensitivity analysis to these parameters and their interaction would be dependent on the assumed hierarchy of resource allocation. Indeed, the variation in allocation assumed at one level of the hierarchy affects the variation at the subsequent levels which, in turn, influence the direction and the rate of the selection response (Worley et al., 2003). These complex effects were revealed with a simple hierarchical model of quantitative genetics (i.e. two hierarchical levels of allocation with a time step of one generation and without interdependency between acquisition and allocation). Tackling the task of a thorough model evaluation seems thus complicated but should none the less be addressed. Despite this, the model behaviour under different simulation scenarios, both selection and environmental variation, fits sufficiently well with the observed phenomena in the literature to suggest that the current model has general validity.

3 Future prospects

3.1 Towards a generic model to manage G × E interactions: the problem of estimating the 'c' allocation components

As noted by Doeschl-Wilson et al. (2006), the standard approach in animal breeding is to record performance traits in individuals and use regression to disentangle the genetic from the environmental influence (Figure 4-4, top). The idea of using a mechanistic approach is to take the problem the other way around; start from a genetic description of the model free from environmental influence and then independently simulate the phenotypic response to environmental inputs (Figure 4-4, bottom). The traits that describe genotypes are intended to be closely related to the biology (the genes) underlying the performance, so to be more stable across environments (Bourdon, 1998; Knap et al., 2003). This opens the appealing possibility to generalize the use of the model to a range of situations.

Still, the problem of estimating the heritable traits included in the mechanistic models remains. This is clearly a difficult task. Techniques of model inversion have been proposed and successfully applied to describe the growth of pigs (Knap et al., 2003; Doeschl-Wilson et al., 2007). These techniques could be considered at the whole animal level based on the description of the genotype proposed in this thesis or another mechanistic description (Figure 4-4, down). In particular, it could be used to test the validity of some model assumptions. As noted by Bijma, (2009), the outcomes of a resource allocation model result from the a priori decision of treating allocation parameters as underlying heritable traits. For instance, no genetic correlation was a priori assumed between these heritable traits of resource allocation. Instead, the observed genetic correlations were a consequence of the combinations that could develop during selection given the resource conservation constraint of resource allocation (i.e. $0 \leq c \leq 1$). This view may overlook the importance of genetic effects of pleiotropy between the traits of allocation independently from the resource constraint, although it could be argued that such pleiotropy is the evolutionary result of prior resource constraints (Stearns, 1992).

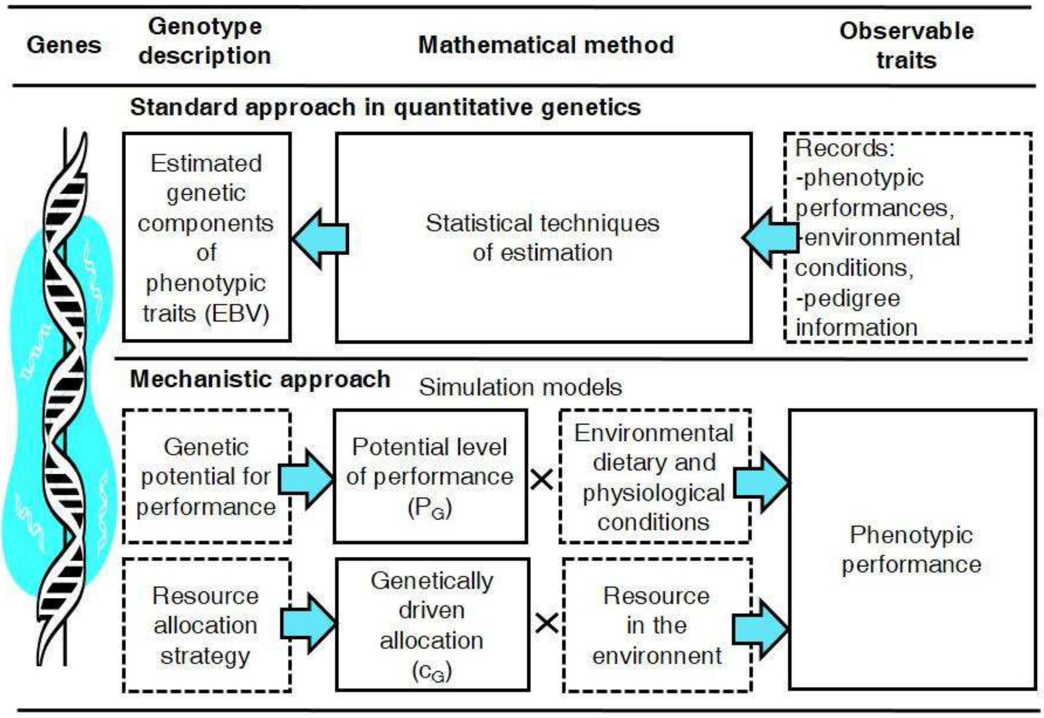

Figure 4-4: Representation of the different approaches to the link between phenotype and genotype and the place of the proposed approach of the thesis in this representation. Boxes with dotted lines are model inputs and those with continuous lines are model outputs. Adapted from Doeschl-Wilson et al. (2006)

3.2 Scale issue for the design of sustainable management systems

The model presented in this thesis focused on the herd level and was developed from an animal production perspective (Figure 4-3b). Still, opportunities to exploit G × E interactions are also within the scope of interest of geneticists. The selection of males with improved genotypes and dissemination of their gametes is a major determinant of the production improvement within the herd (Figure 4-3a). However this view implies representing herds at a population scale. In the real world, herds rarely completely fit one of the views proposed (Figure 4-3ab). They rather represent intermediary situations between the two, i.e. they usually generate genetic progress within the herd based on selection of both home-bred genotypes and imported germplasm from breeding companies. This suggests that different levels and processes could be used in conjunction to exploit G × E.

To avoid the risk of a mismatch between the selected genotypes and a particular farm environment, some authors have proposed to customize the global selection index used in breeding schemes to fit the local farm conditions (Bowman et al., 1996; Calus et al., 2005). For this, herd descriptors are required to characterize the local herd environment. These descriptors should be a priori independent from genetic factors (Huquet et al., 2012a), which is not the case for instance when herd milk production is used as descriptor. The approach proposed in this thesis simulates a selection response on a genetic basis, a priori independent from the environment. It could be thus further developed to identify what would be the most relevant herd descriptors to be used.

3.3 Towards another research approach iteration: *describe* the herd environment and *explain* its dynamic

Describe

From the perspective of large scale genetic improvement, synthesizing descriptors of the herd environments are desired to be easily included in the statistical techniques of estimation (Calus et al., 2005). However, from a herd system perspective synthesizing descriptors may not so be desirable as they may smooth away important variation between management environments. This variation may arise from differences in the local herd environments such as for instance the geographical location of the farm, the feed regime or the kind of system (e.g. conventional or organic). These features are expected to be to some extent correlated which should make easier the use of a synthetic descriptor. However, the way they correlate will crucially depend on the manager. Moreover, farmers may have different priorities/styles of management, as have been reported in the characterization of culling practices (Beaudeau et al., 1996; Ahlman et al., 2011). Differences in the culling criteria may also result in different weightings of traits in the breeding goal and obscure the detection of G × E effects among different herds. From this perspective, it would be crucial to carefully consider the role of the manager who sets the selection criteria and on-farm strategy, modulates or not the herd environment, and can create “local” environments that match animal genetic expression through time.

Explain

In this thesis, we set out to represent G × E interaction as a multi-level dynamic process that involves the farm manager, rather than as a statistical term. Although this was achieved at the animal level, the influence of the farm manager on this interaction has not been developed to any significant level of sophistication. The nutritional responses (i.e. the observed phenotypes) at the animal level were simulated within a fixed management strategy. Based on these responses, animals were also selected with fixed criteria. Now, what if management adaptation was added to the model? For instance, provided that animals display heterogeneous desired intakes at a given time, one could hypothesize that if the farm manager exploited this by a judicious reallocation of the feed resources between animals (i.e. representation of differential management within the model simulation), maybe the trade-off between milk yield and survival would not appear, or would take a different shape.

In brief, studying thoroughly the exploitation of G × E interactions by the farm manager would require representing *how* the manager can influence production and selection as an on-going process, adapted according to prevailing conditions. At the present stage of development, the model merely provides some basis for this. The crucial missing piece is a better description of the decisional process and its interaction with the biophysical processes.

Given the central importance of, and variability in, decisional processes it would be clearly valuable to be able to describe and even quantify them. Indeed a wide diversity of tools have been proposed, which are often associated with different considerations of the decisional component (Cerf et al., 2009). Moreover, some concepts such as the ‘management style’ have generating encouraging outcomes for the perspective of capturing the driving management factors behind the diversity of farms trajectories (van der Ploeg, 2003). It would be particularly challenging but useful to describe these factors such that they could be integrated with herd environment factors, and time. Addressing such a complexity seems a promising avenue for identifying emergent properties and *in fine* indicates the key entry points for the design of sustainable options in a particular herd. So far this thesis has stressed the evolution of animal’s priorities during selection. We believe that it would now be useful to know how these priorities co-evolve with those of the farm manager, so as to quantify the risk of mismatch between the genotypes and the herd environments.

PAPERS

Paper 1

A resource allocation model to better understand the consequences of genetic selection on dairy herd performance

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In revision for the *Journal of Animal Science*

ABSTRACT

Single trait selection for production increases environmental sensitivity, which causes problems especially when animals selected in a non-constrained environment are transferred in local farm environments with varied levels of constraint. The herd environment affects the type of animal that is favored across generations, as a consequence of the local selection objectives, and within generation across lifetime, as a consequence of the nutritional management. To better understand how the interaction between these 2 components influences the development of environmental sensitivity within a herd, an individual-based model was proposed and used to simulate the long-term consequences of different selection strategies. To account for the trade-offs between life-functions that potentially emerge as a response to selection, a key assumption was to set heritability at the level of the resource allocation coefficients in the nutritional sub-model. Weekly outputs of this sub-model were used to calculate the performance traits under selection. Two single trait selection strategies (milk production only and production efficiency only) and one multi-trait strategy (milk, body condition score and age) were used to select individuals chosen to be parents in the herd every year. Long-term selection responses in a constant environment illustrated the model sensitivity to different selection strategies. Both single-trait selection strategies led to a steady increase in milk yield but had negative impacts on BCS and reproduction rate but they relied on different genetic changes to resource allocation across generations. Animals selected solely for milk production became larger which increased their acquisition capacity but they were dependent on unlimited resource availability to maintain survival rates. Animals selected for production efficiency allocated more resources toward lactation which compromised survival but they were less sensitive to a resource shortage. Finally, the multi-trait selection strategy resulted in a robust performance but it came at the cost of a slow rate of milk yield genetic progress. Simulation results provide proofs-of-principle that setting heritability at the level of the resource allocation facilitates representation of the effects of both the environment and the selection strategy on within lifetime temporal pattern of performance, without using genetic parameters for performance levels per se.

Key words: Resource allocation, Selection, Herd environment, Lifetime performance

INTRODUCTION

Single trait selection for production works spectacularly if simultaneously the animals under selection remain relatively non-constrained by the environment (Kelm and Freeman, 2000). Based on a modeling approach, Van Der Waaij, (2004) showed that selection solely for production could lead to environmental sensitivity by influencing the resource allocation between life-functions across generations. Additionally, herd management decisions to modify nutritional inputs have differing consequences on lifetime performance according to the type of individuals in the herd (Puillet et al., 2010). Overall, these results indicate that the herd environment may affect the type of animal that is favored across generations of selection, as a consequence of the local selection objectives, and within generation across lifetime, as a consequence of the nutritional management.

Obviously, these intra and inter-generational consequences are also interdependent. Nutritional responses are well recognized as being regulated by genetic drives (Bauman and Currie, 1980; Chilliard et al., 2000). Theoretically, this component should be thus partly inherited from parents to offspring. In turn, within-life performances shape the response to selection, in particular through their effects on reproduction and survival rates. Such interdependency is expected to influence the development of environmental sensitivity within a particular herd, and possibly the re-ranking of genotypes across environments. To investigate this, the model presented in this paper tackles the issue of integrating the dynamic regulation of nutrient partitioning across lifetime with genetic parameters inherited between generations. The aim of this study is to contribute insight on the development of associations between traits, as a consequence of both an animal's resource allocation across its lifetime, and the long-term selection based on one or more performance outcomes by the farm manager.

MATERIAL AND METHODS

Model Overview

Figure 1 presents the main processes that make up the herd simulation model developed in this study. The model is individual-based and combines a weekly cycle, which represents the nutrition process, with a yearly cycle, which represents selection and mating processes.

Using a 1-week time-step, the individual animal sub-model simulates the responses to the nutritional resource inputs. For each individual, nutrition is viewed as a resource partitioning process controlled by allocation coefficients under genetic influence. These parameters represent the part of the nutritional mechanism that is inherited from parents to offspring, and which then mediate genetic progress in performance when selective breeding is practised over several generations. These parameters are integral to partitioning functions which depend on animal age and reproductive stage. The nutritional responses obtained as outputs describe a phenotypic variability in survival (i.e. risk of mortality), reproduction (i.e. probability of conception) and performance (i.e. resource intake, body weight, milk production and litter size). Every week, these individual performances can be then recorded and used as evaluation criteria for annual selection of parents.

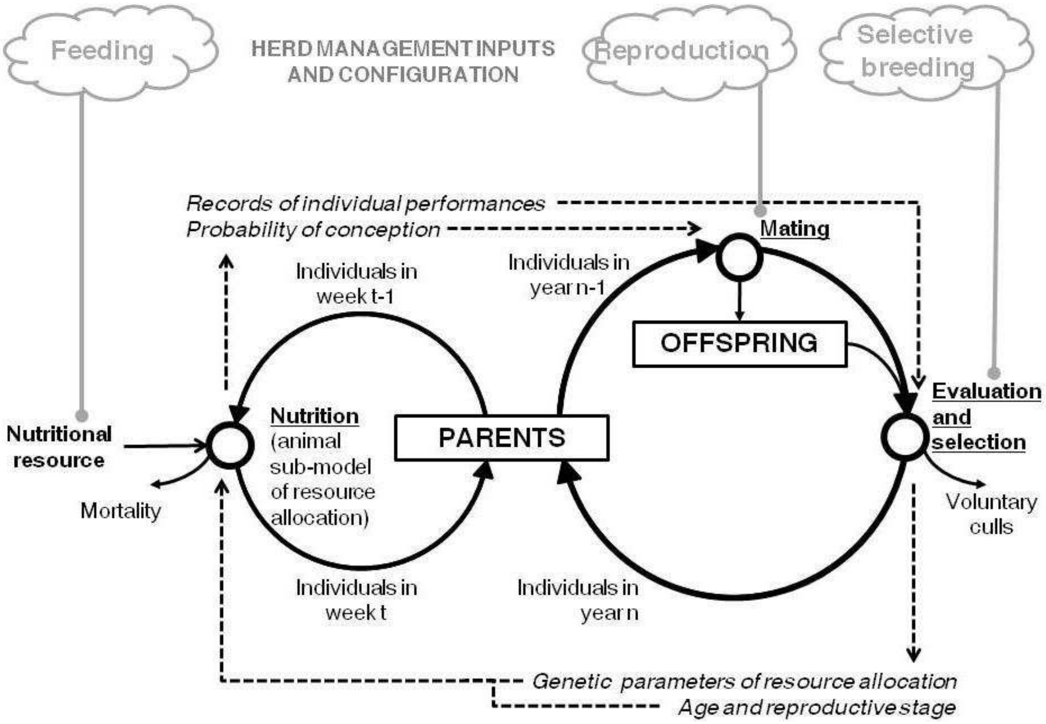


Figure 1: Overview of the 3 main processes that make up the herd simulation model. The nutritional responses of individuals chosen to be parents are represented on a weekly basis (small cycle). It determines their individual survival (i.e. the risk of involuntary culling), their probability of conception during the mating process and their performance. These performances, in turn, are used during the evaluation/selection process. Mating and selection processes are represented on a yearly basis (large cycle). It determines reproductive success and distinguishes those individuals that are selected to become parents from those that are voluntary culled and replaced. These 2 processes, in turn, lead to differences of age and reproductive stage that affect the nutritional responses. The grey clouds and connectors indicate where herd management decisions affect the 2 interdependent cycles. Other symbols represent compartments of individuals (boxes), physical flows (solid black arrows), information flows (dotted arrows) and processes (circles).

Each year, surviving individuals are evaluated for their observed phenotypic performance recorded in year n−1. The best ones are selected to be parents in year n, whereas the others are voluntarily culled. The manager’s selective breeding strategy defines the rate of voluntary culling (i.e. the selection pressure applied to the candidates), and the selection weights (i.e. the importance given by the manager to the different criteria used to evaluate and rank the candidates). Outputs of the evaluation/selection and mating processes induce individual differences of age and reproductive stage that affect the nutritional responses. Individual offspring in year n, have inherited values for resource partitioning parameters from their parents during the mating process in year n−1. Every year, the selection of replacements by the manager is simulated so as to maintain herd size. This along with inherent variation in individual animal survival and fertility bring about genetic progress in the herd.

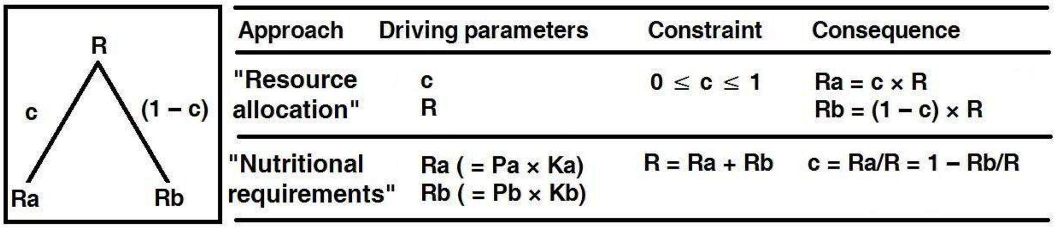
As a whole, the model accounts for 3 sources of individual variability that depend on herd management inputs: i) genetic variability implemented at the level of nutrient partitioning and which depend on the selection weights used in the selective breeding strategy, ii) environmental variations modelled through the level of the nutritional resource provided, and iii) time variations between individuals due to differences of ages or reproductive stages depending on mating and the rate of voluntary culling used in the selective breeding strategy. As the focus of the present study was on testing contrasting selection strategies, most emphasis was placed on the genetic component of individual variability. Herd management was thus configured to restrict individual variability related to either the environment or differences of ages or reproductive stage.

The first major issue to address in such a model was to determine which partitioning parameters of the nutritional resource should be assumed to be under genetic influence (Friggens and Newbold, 2007). Given the increasing evidence for negative genetic correlations between milk production and others life functions, a prerequisite for this model was to choose genetic parameters that would allow trade-off between life functions to become apparent as a response to selection.

First, a rationale for a genetic description of resource partitioning is provided for the development of the animal sub-model that is described thereafter. Model initialization at the herd level is then presented, as well as the herd management inputs and the configuration of the evaluation/selection and mating processes used in this study. Finally, the simulation experiments are presented.

Rationale for a Genetic Description of Resource Partitioning

A simplified representation of resource partitioning is used to represent candidate parameters that may be subject to genetic control. In Fig. 2, a quantity of resource (**R**) is obtained by an animal and split into 2 quantities (**Ra** and **Rb**) respectively used for 2 traits (**a** and **b**). Here, the animal is taken as being in an ideal environment that is no way constraining (i.e. a non-limiting resource provision).



Approach	Driving parameters	Constraint	Consequence
"Resource allocation"	c R	$0 \leq c \leq 1$	$Ra = c \times R$ $Rb = (1 - c) \times R$
"Nutritional requirements"	Ra (= Pa × Ka) Rb (= Pb × Kb)	$R = Ra + Rb$	$c = Ra/R = 1 - Rb/R$

Figure 2: A simplified representation of resource partitioning and 2 different approaches for genetic control in a non-limiting environment. The "resource allocation" approach, used in this study, implies a genetic control of resource partitioning at both the level of resource acquisition (R) and the subsequent allocation (c) of this resource between traits (Ra and Rb for traits a and b respectively). Alternatively, a nutritional requirements approach would imply a control of resource partitioning at the level of the traits themselves by defining requirements (Ra and Rb) as a result of genetic potentials (Pa and Pb) multiplied with some nutritional constant (Ka and Kb) (see text for details).

The approach adopted in the present study was to define the resource allocation coefficient (**c**) under direct genetic control and R as being another control variable in the model. Evidence from life history biology suggests that fitness costs, and possibly morphological constraints, are associated with increasing resource acquisition (Reznick et al., 2000). Here, genetic limits to R, the amount of resource acquired, are thus assumed. As a corollary, the resources allocated (Ra and Rb) and the resulting performances for traits a and b are always a consequence of both c and R. This is different from the approach generally adopted in most of the models used to predict farm animals' intake and performances, because usually the assumption is that genetic control resides solely in potential performance. In that case, Ra and Rb are seen as nutrient requirements derived from the genetic potentials of performance (**Pa** and **Pb)**, e.g. a milk yield potential, multiplied by some nutritional constants (**Ka** and **Kb)**, e.g. the amount of MJ required to produce a kg of milk (Emmans and Kyriazakis, 2001). The resource supply needed to satisfy both requirements is equal to their sum, R = Ra + Rb, and its partition, being simply c = Ra/R, would be a consequence of the genetic potentials Pa and Pb. The important point is that the resource allocation coefficients and the performance potentials cannot simultaneously be under genetic control so the 2 approaches are mutually exclusive.

Under the resource allocation approach, assuming a limited amount of resource available (R) implies that selection for an increase in one function (e.g. lactation) will create a trade-off, i.e. a genetic change in c (Williams, 1966; Stearns, 1992). Originally, resource allocation models have been developed in the context of wild animals with the assumption of an extrinsic limitation on the resource available. This seems reasonable given the constraints imposed by the natural environment, but unlikely in a livestock breeding context where a high quality diet can be distributed in large quantities. Intrinsic limits to energy intake have thus to be considered here. From experimental biology, 2 main hypotheses received attention for explaining such limits (Speakman and Król, 2011). One hypothesis is that intake reflects the summed demands of individual peripheral tissues, such as the mammary gland, which have their own limited capacity (Hammond et al., 1996b). This supports the idea of potentials, as introduced in the nutritional requirements approach. An alternative hypothesis suggests that the main limiting factor on intake is simply the capacity of the alimentary tract to absorb energy (Weiner, 1992). This is in line with the idea that some process limits or determines intake, and that acquisition limitation, as introduced in the resource allocation approach, can merely be the expression of that process (Illius et al., 2002). Evidence has been found for a possible mechanism for control of intake that is influenced via body lipid reserves and that applies for organisms as different as rats and sheep (Stubbs and Tolkamp, 2006; Tolkamp et al., 2007). Animals are prepared to deposit and defend larger or smaller body reserves depending on food quality suggesting they integrate the signals from body reserves and feed quality to control energy intake. Such a view is congruent with the current view on energy balance during the reproductive cycle of dairy females (Friggens, 2003; Friggens et al., 2004) whereby a genetically driven pattern of body reserves is closely related to the notion of a "defended" level of body reserves by the animal.

For the resource allocation approach, the representation of trade-offs between functions relies on a distinction between the resource acquisition from its subsequent allocation whereas in farm animal science, these 2 notions are classically blended into the notion of potential performance. Evidence from the literature has provided the rationale for this. Therefore, the animal sub-model described below is built on the assumption that resource acquisition (R) and allocation (c) are controlled separately (but not necessarily independently), and that the heritability is at the level of the allocation coefficients and not at the level of potential performance.

Animal Sub-Model Description

Resource Acquisition. Resource intake was assumed to have an upper limit that represents the desired acquisition potential of the animal, here called $\mathbf{R_G}$, expressed as ME (in MJ/d). Considerable evidence shows that ME intake is linearly related to body weight across species. This suggests some kind of structural relationship with animal size, here approximated by non-labile body weight (**BWnl**, kg). Accordingly, a basic level of resource acquisition potential, $\mathbf{R_{G0}}$, linearly related to BWnl was defined as:

$$\mathbf{R_{G0} = a \times BWnl.}$$

To account for the postpartum increase in resource acquisition potential and its subsequent decrease during the reproductive cycle of the female, a genetically driven component, **R_GOff**, was added to **R_{G0}**. The conceptual basis for this component was to assume an evolutionary drive for supporting the growth of current offspring (via lactation), and a progressive natural weaning thereafter (see details in Appendices).

In addition, the notion of a defended target of body fatness (**BCS*)** was included (Tolkamp et al., 2006), such that the desired resource acquisition was adjusted according to **BCS** (0 to 5 points scale). This was defined as follows:

$$\mathbf{R_G = R_{G0} \times (1 - b \times (BCS - BCS^*)).}$$

Body fatness had an effect of decreasing R_G when BCS was greater than the target level BCS*, and increasing R_G when BCS was less than BCS*.

Whether the total amount of resource obtained (**Robt**, in MJ/d) equals R_G or not depends on the nutritional environment and the amount of energy mobilized from body reserves (**BR**). For animals fed ad libitum, the amount of energy obtained from the environment (**$Robt_E$**) is mainly determined by the diet quality. For simplicity, a global diet quality factor, **Q_E** (between 0 (poor) and 1 (excellent)) was defined as the proportion of R_G obtained when the diet was provided ad libitum. When the diet quantity was limited in the environment, the amount of resource available for each animal (**R_E**) may be less than the desired amount $R_G \times Q_E$, so the amount $Robt_E$ (MJ/d) was determined by the most limiting factor:

$$\mathbf{Robt_E = \min (R_G \times Q_E, R_E).}$$

The degree of environmental limitation was defined at the level of a class of animals (basically 2 classes being either less or more than one year of age), as the proportion **P_{LIM}** of this group not fed ad libitum. For this, the group distribution of the desired intake R_G for a resource of quality Q_E was considered (i.e. $R_G \times Q_E$), and the constant amount of resource available to each animal, R_E, was defined as the value of $R_G \times Q_E$ equal to the P_{LIM}^{th} percentile of this distribution.

Body reserve mobilization is genetically driven after parturition (Friggens et al., 2004) and is possibly environmentally driven in the case of a nutritional constraint as part of the regulation of homeostasis (Chilliard et al., 2000). These 2 components were taken into account in this model. The rate of genetically driven mobilization (**$Rmob_G$**, MJ/d) was assumed to decrease exponentially with time of lactation and its level was positively associated with the level of BR at parturition (Friggens et al., 2004). The rate of environmentally driven mobilization (**$Rmob_E$**, MJ/d) was assumed to increase with the level of nutritional constraint and to be bounded to a maximum rate which is size dependant. The level of nutritional constraint was quantified with the ratio **SAT** (uniteless), defined as follows:

$$\mathbf{SAT = Robt_E / R_{G0},}$$

and this was used as a modifier of $\mathrm{Rmob_E}$. The resulting amounts of resource mobilized were added to $\mathrm{Robt_E}$ in Robt:

$$\mathbf{Robt = Robt_E + Rmob_E + Rmob_G.}$$

Resource Allocation. Once Robt has been determined, the model allocated it between the different animal functions: BR deposition (Rdep), pregnancy (Rpreg), lactation (Rlact), growth (Rgrow) and survival (Rsurv). The assumed hierarchy of resource allocation shown in Fig. 3 is based on the elementary representation in Fig. 2 which was repeated for each level of the hierarchy. Thus, a proportion (c) of the resource available for allocation at one level (R) was allocated to the function at that level, whereas the remaining part ((1 – c) × R) was available for allocation at the next level down. In the chosen hierarchy (Fig. 3), the 5 different functions were ranked according to their degree of dependency on the nutritional environment. Body reserves deposition and pregnancy are considered to be quite dependant on the environment (they are activated only when the conditions are favorable) whereas growth and survival are considered as necessary functions (they are activated whatever the environment). At each level, the allocation coefficients **d**, **p**, **l** and **g** were constructed according to a general model (c) which combines a genetically driven (c_0 × $\mathrm{cmod_G}$**)** and an environmentally driven ($\mathrm{cmod_E}$) modifying component to the resource allocation coefficient, thus:

$$\mathbf{c = c_0 \times cmod_G \times cmod_E.}$$

A basic component (**c_0**) of the genetically driven allocation, constant throughout the animal's lifetime, was modified by a time-component (**$\mathrm{cmod_G}$**, between 0 and 1, see details in Appendices) representing the temporal changes in relative priorities between life-functions (Martin and Sauvant, 2010). Environmentally driven modifications (**$\mathrm{cmod_E}$** between 0 and 1) were represented by a decrease in resource allocation coefficients when the nutritional constraint becomes high and survival is potentially compromised. The degree to which the allocation can be decreased in favor of survival according to the level of nutritional constraint (SAT), was used to characterize environmental sensitivity. A general sigmoid function was used for the environment-modifiers $\mathrm{cmod_E}$ such that $\mathrm{cmod_E}$ ranges from 0 when SAT = 0 to 1 when SAT = 1:

$$\mathbf{cmod_E = 1 / (1 + exp(- 15 \times (SAT - SATc_0)),}$$

where parameters **SATc$_0$** indicate the point of inflexion for each allocation decrease (i.e. **SATd**, **SATp**, **SATl**, and **SATg** for deposition, pregnancy, lactation and growth respectively). Thus genotypes with high (vs. low) values of SATc at a particular level of the hierarchy, are expected to have a plastic (vs. robust) resource allocation for this level.

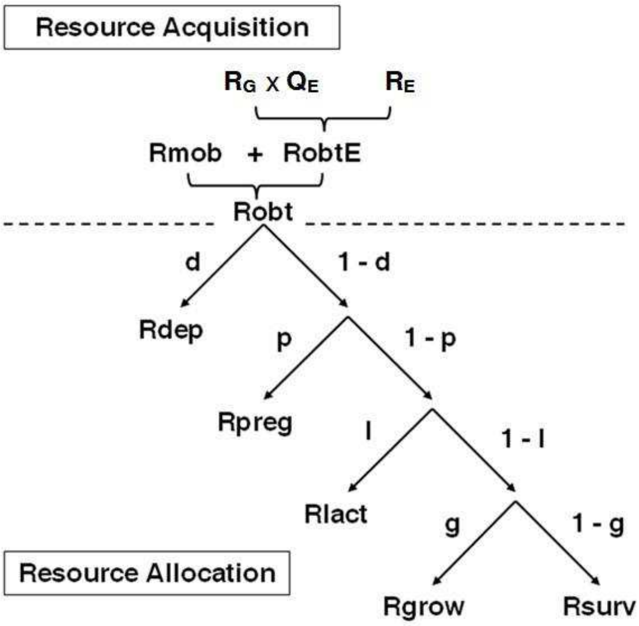


Figure 3: Schematic representation of the resource acquisition process and the hierarchy of resource allocation between functions. The animal has a potential for resource acquisition (R_G) which is achieved or not depending on the resource quality (Q_E) and the resource availability in the environment (R_E). The sum of resources obtained (Robt) from the environment ($Robt_E$) and from the body reserves (Rmob), is then allocated between body reserves deposition (Rdep), pregnancy (Rpreg), lactation (Rlact), growth (Rgrow) and survival (Rsurv). At each level of the hierarchy, coefficients d, p, l and g describe the proportion of the available resource which is allocated, and the remaining proportion available for the next level down. In the case of nutritional constraint (i.e. a decline in Robt), some allocation plasticity allows the coefficients to be decreased to give priority to survival. In this case, the proportion of Robt which is allocated to survival is increased ($s = (1 - d) \times (1 - p) \times (1 - l) \times (1 - g)$).

Model Initialization

Genetic variation was implemented at the level of the allocation coefficients for BR deposition (d) and lactation (l). The basic components, **d$_0$** and **l$_0$** respectively, were chosen to represent variation in the genetically driven part of the allocation, and parameters SATd and SATl to represent the environmental sensitivity of these allocations. Phenotypic population means were 0.25 and 0.75 respectively for d_0 and l_0, and 0.5 for both SATd and SATl. A phenotypic SD of 0.05 and a h^2 of 0.3 were used for all of the 4 parameters. Initial TBV of these 4 traits were simulated in a base population of and TBV of any new individual were then simulated from those of their parents (see details in the Appendices). To respect the constraint on coefficients d_0 and l_0 (i.e. must be between 0 and 1), phenotypic values sampled initially from normal distributions were transformed with a logistic function. All others parameters of the animal sub-model were constant during the time of simulation. Their values were calibrated with average data for a dairy goat fed ad libitum with a high quality diet (Fig. 4).

Genetic variation in resource acquisition (R_G) comes about indirectly through the implicit relationships among the energy partitioned off for lactation and BR deposition, and the remaining energy available for growth (Fig. 3). In this way, animals that partition less energy into lactation and BR deposition will have more energy available for growth, leading to a larger BWnl throughout the life of the animal and therefore greater rates of R_G. Further, because R_G is dependent also on BCS (i.e. the level of BR relative to BWnl), genetic variation in R_G also comes about indirectly through genetic variation in parameter d. With low levels of d, the animal has lower body energy reserves, and as a consequence R_G will be greater.

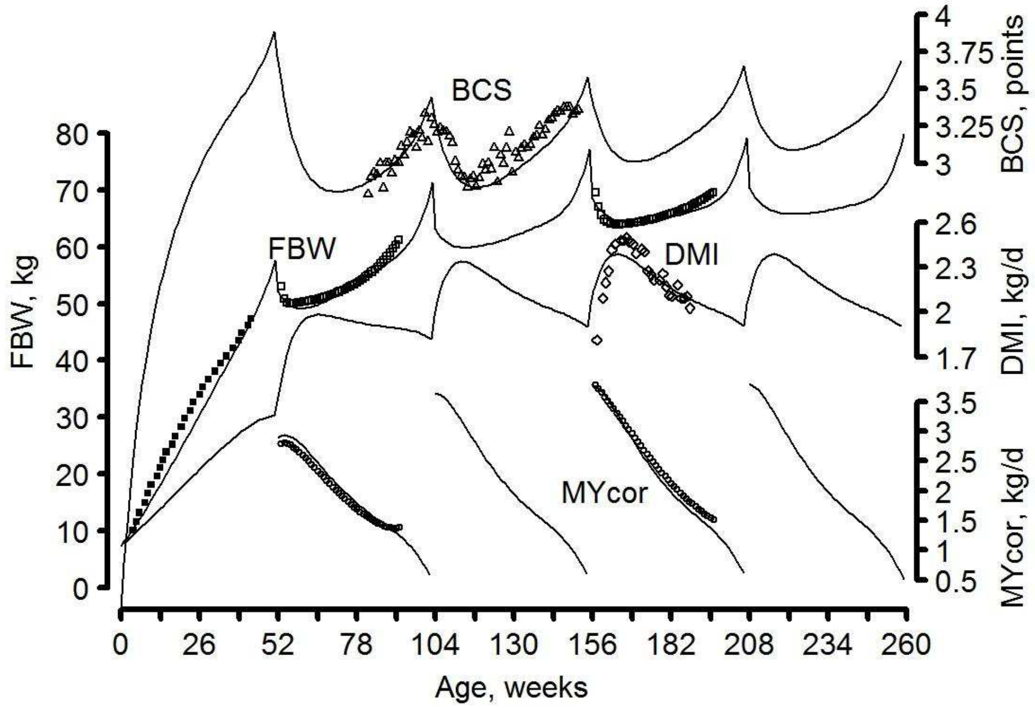


Figure 4: Model simulations (continuous lines) of full BW (FBW), BCS, and energy corrected milk yield (MYcor) from birth to 5 years (i.e. 260 weeks) of life. Symbols are data used for model calibration: Sauvant et al., 2012 (○ and □); Puillet, 2010 (■); Sauvant and Morand-Fehr, 1982 (◊); Douhard et al., unpublished data (Δ).

Animal sub-model outputs were simulated on a time step of a week. Energy corrected milk yield (**MYcor,** in kg/d), and mass variations of BWnl, BR and of the gravid uterus were calculated from the different amounts of energy allocated (Rlact, Rpreg, Rgrow and Rdep) and the total energy mobilized (i.e. RmobE + RmobG), assuming constant ME conversion factors (see details in the Appendices). Empirical relationships were used to estimate the full BW (**FBW**) and BCS from the simulated values of BR and BWnl. The number of offspring reared (between 1 and 3) was positively influenced by the cumulated energy allocated to the gravid uterus during pregnancy. Survival was stochastically determined from a survival likelihood (**SURV**). This likelihood transits from a low (0) to a high (1) level when Rsurv increases relative to a basic level **$\mathbf{Rsurv_0}$**. A standardization of Rsurv with respect to $BWnl^{0.75}$ was undertaken (**$\mathbf{Rsurv_{st}}$**) to account for the effects of size on the costs of maintenance. Additionally, an age-dependent term was introduced to reflect animal senescence as characterized by an exponential rate of decrease (**kage)**.

$$\mathbf{SURV = (1 / (1 + exp(- 15 \times (Rsurv_{st} - Rsurv_0))) \times exp(- kage \times age).}$$

Conception was stochastically determined from a conception likelihood (**CONC**) following the approach proposed by Friggens and Chagunda (2005). The main determinants of CONC are the BCS level relative to a base level, **$\mathbf{BCS_0}$**, and a modification to this base level determined by the rate of change in BR (**dBR**) proportionally to some scaling factor (Xd_{BR}):

$$\mathbf{CONC = 1 / (1 + exp(- 2 \times (BCS - (BCS_0 - X_{dBR} \times dBR)).}$$

The model starts out with a newborn base population, and initialisation was undertaken for a period of 20 years with a fixed replacement rate to keep a constant herd size. For this initialisation period, voluntary culls were chosen randomly allowing equilibrium in both herd demography, as well as in average performances to be established.

Herd Management Configuration and Inputs

In this study, to restrict individual variability related to either the environment or herd management, the feeding and management calendars were fixed.

Mating. The mating period occurred only during week 33 and implied a kidding period at week 1 of the year after. Breeding does subject to voluntary culling or death were replaced with female kids simulated from the previous year at a constant time point that was 8 weeks after the kidding period. During the mating period, every female was assigned randomly one male among those available for reproduction.

Selective breeding. Selective breeding defines the rate of voluntary culling and the selection weights. There were 3 possible culling reasons: if living females reproduced successfully during the year they could be voluntary culled due to selection on trait performance. Unsuccessful reproduction resulted in automatic voluntary culling. Females that did not survive during the year were considered as being involuntary culls. Performance based voluntary culling was set at a constant rate of 25% during selection. Young individuals chosen for replacements came from the herd and were sons and daughter of the elite adult females (i.e. pedigree selection). Their number was determined to keep constant the total herd size (i.e. the number of individuals just after selection), here set at 500 females and 10 males. The 10 males were fully replaced every year.

The selection weights were part of a general selection index (**SelIndex**) used to evaluate candidates, rank them and decide on which ones would be selected every year:

$$\mathbf{SelIndex = W_{PROD} \times PROD + W_{COND} \times COND + W_{AGE} \times AGE,}$$

where **PROD, COND and AGE** are different criteria calculated from candidates performances and where **W_{PROD}, W_{COND} and W_{AGE}** are selection weights defined by the herd manager for a particular selection strategy. The production criteria (PROD) was defined either as a yield measure, i.e. the maximum energy corrected MY observed during lactation (MILK, in kg/d), or as an efficiency measure, i.e. the ratio between MILK and the full BW observed post partum (FBW, kg). The full BW was taken here as a proxy of resource acquisition. Penalties on adult live weight are common in selection indexes for ruminants to account for the higher feed requirements of large mature size animals. COND was defined as the average BCS simulated during the year. AGE was the age of the candidates at the time of selective breeding. To homogenise the different criteria units and avoid scale effects, MILK, the ratio MILK/FBW and COND were expressed as standardized measures (z-values). As primiparous females are still developing when they are evaluated, standardization was undertaken separately within primiparous and multiparous females.

Simulation Experiments

Two kinds of simulation experiments were carried out. Firstly, 40 years of selective breeding were simulated for 3 different strategies in a favorable environment. Feed resource was of constant high quality ($Q_E = 0.85$) and distributed ad libitum ($P_{LIM} = 1$). Secondly, environmental sensitivity was tested by observing the effect of transferring the 3 selected herds of year 40 in environments with a limited resource available R_E ($P_{LIM} < 1$) in year 41.

The 3 different selection strategies were simulated with 20 herds replicated in each one. Two strategies were based on single-trait selection for production (**ST1** and **ST2**: $W_{PROD} = 1$; $W_{COND} = 0$, $W_{AGE} = 0$), evaluated either as yield (ST1) or as efficiency (ST2). The third strategy was multi-criteria (**MT**), based on MILK, COND and AGE (MT: $W_{PROD} = 1$; $W_{COND} = 0.5$, $W_{AGE} = 0.5$). In addition to the individual performances included in SelIndex, a survival and a reproduction rate were calculated at the herd level. Survival rate of year n was defined as the proportion of individuals that survived from year n to year n + 1. Reproduction rate was defined as the proportion of these living individuals that reproduced successfully during year n. Phenotypic means of parameters under genetic influence (d_0, l_0, SATd, SATl) were calculated over all the replicates between strategies. Data were analyzed by using one-way ANOVA and paired comparisons were assessed at $P \leq 0.5$ with Tukey's test.

Environmental sensitivity was tested as the yearly response in average MILK, survival and reproduction rates to a range of environmental limitations. The different degrees of environmental limitations were defined with P_{LIM} applied to the whole animal population made up of the 3 selected herds at year 40. Ten degrees of environmental limitation were tested with P_{LIM} ranging from 1 to 0.1.

RESULTS

First, the progression in the level of the different culling reasons is reported to describe the herd demographic context in which the average individual progress is achieved. This progress is then described for the different selection strategies, together with the underlying changes in resource allocation. The last part of the results represent how, the different breeding objectives shaped the herd dynamics during the selection process and how the herds resulting from 40 years of selection in a favourable environment would respond if suddenly transferred to a limiting environment.

Herd Demography

Figure 5 shows the 3 selection strategies had different progressions in the level of culling due to selection by the manager (i.e. performance based culling) and the level of culling due to biological reasons (i.e. reproductive failure and mortality). In all the strategies, the increasing replacement rate was largely explained by the number of living females that failed to reproduce during the year. This was particularly apparent for the 2 single-trait strategies (ST1 and ST2). Failure to reproduce accounted for 20% of the total culls at the beginning of selection but then increased linearly with single trait selection until reaching a limit at about 65%. The number of culls decreased thereafter because of reduced herd size. ST2 was relatively more affected by mortality (28% vs. 20% for ST1 and 22% for MT). Apart from the trend observed in these single trait strategies, the progression was also increasingly variable, especially during the last 5 years (SD over replicates ≈ 6.1% for ST1, 4.7% for ST2).

For the MT strategy, the level of culling due to biological reasons increased only very modestly, so the level of performance based culling could be maintained throughout years.

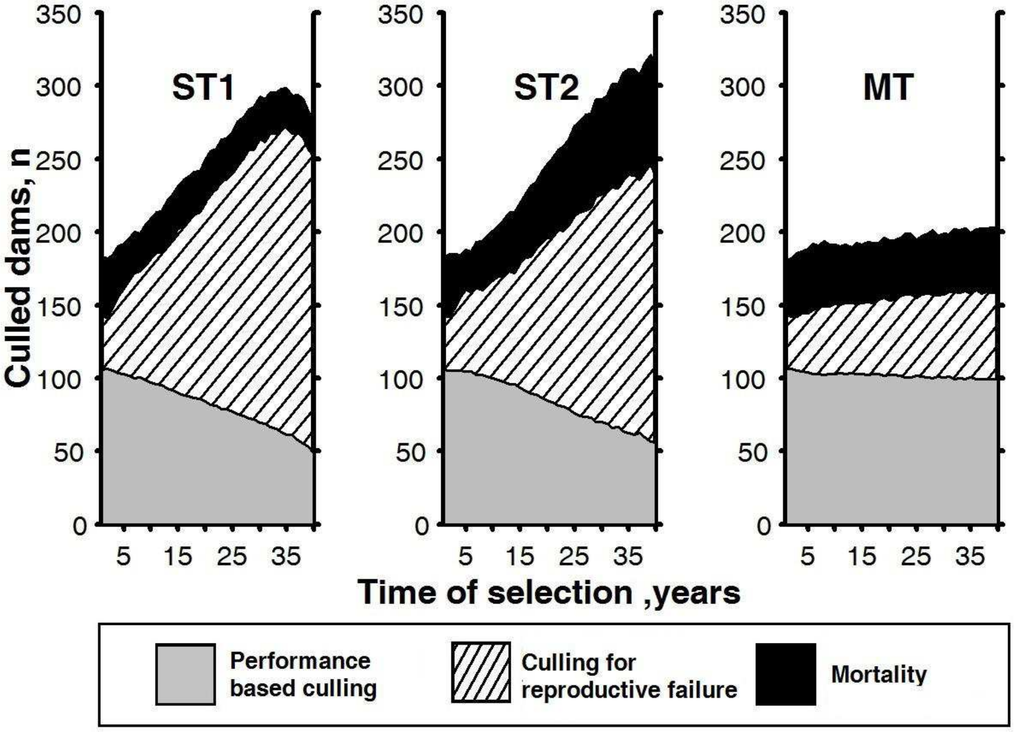


Figure 5: Number of culled dams every year and culling reasons. During 40 years, herds were selected on a single milk trait production, either yield (ST1) or efficiency (ST2), or for a combination of yield, BCS and age (MT). Targeted herd size was of 500 females at the beginning of every year.

Average Individual Progress

For every year of simulation, Fig. 6 shows the average performances of the selected dams in the herds. The underlying changes in resource allocation parameters are presented in Table 1. All the selection strategies led to an increase in MILK and FBW, and to an opposite trend in BCS (Fig. 6). For each strategy, AGE decreased in a pattern that was consistent with the increasing culling rates previously observed (Fig. 5). The high age observed in the MT strategy was also because older females (i.e. those that survived and reproduced successfully during previous years) were systematically preferred to young females except if the difference in milk yield was substantial (W_{AGE} = 0.5 in MT strategy). The decrease in BCS occurred when it was not directly selected against (as was the case for single trait selection strategies ST1 and ST2), and was moderated when it was selected for positively (W_{COND} = 0.5 in MT strategy). The decreasing trend for BCS was associated with a decrease in the resource allocation for BR deposition, ($d_{0,}$ Table 1), in favour of the subsequent allocations in the hierarchy (i.e. pregnancy, lactation, growth and survival, see Fig. 3). Individuals selected for milk only (ST1) had a greater milk yield and were both bigger and leaner, which was consistent with a greater resource acquisition (R_G). In this case, the strong decrease in d_0 was associated with a moderate increase in the resource allocation for lactation l_0 (ST1 in Table 1). Alternatively, when R_G progress was indirectly controlled by selecting on milk production efficiency (ST2) instead of milk production alone (ST1), progress in FBW was lower and selected individuals were younger. In this case, more selection pressure was applied to l_0 (ST2 in Table 1), thus a lower proportion of the resource obtained was partitioned away from lactation towards growth and survival. The low mean age observed in ST2 (Fig. 6) together with the high mortality (Fig. 5) suggest that the moderate increase in resource acquisition potential (R_G) did not fully compensate for the reduction in the proportion of energy allocated to survival and BR deposition.

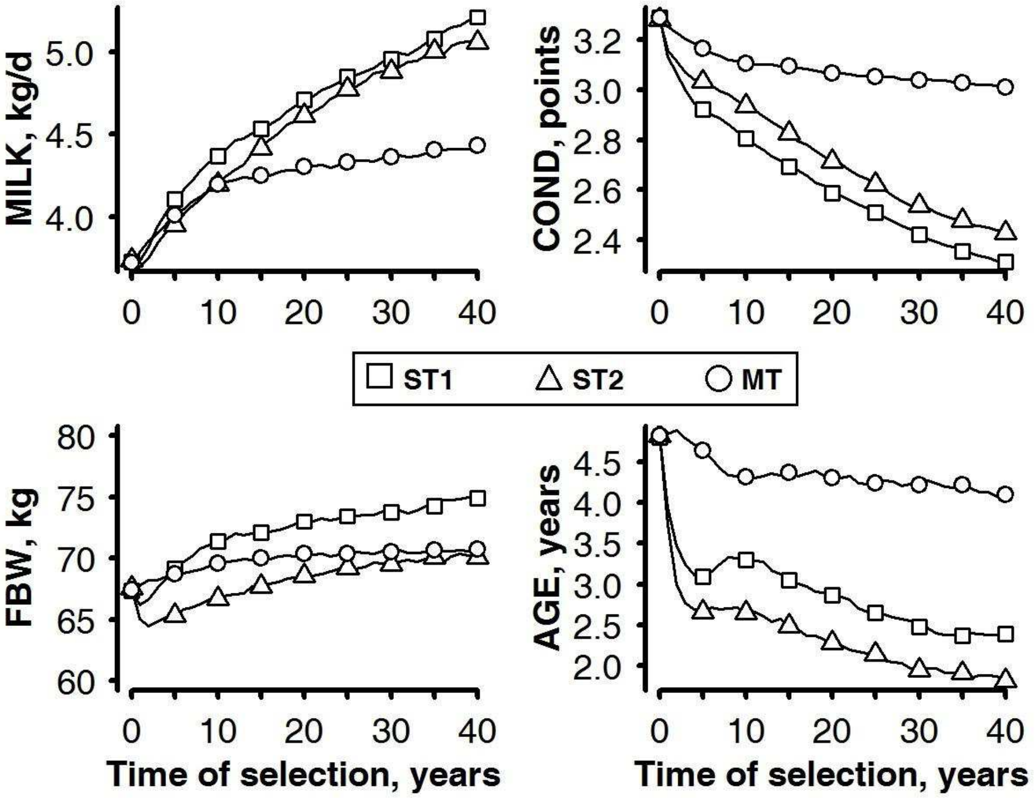


Figure 6: Changes in average values of corrected milk yield at peak lactation (MILK), mean BCS (COND), full BW at parturition (FBW) and age (AGE) for the candidate females selected over 40 years in a favorable herd environment. Selection is for milk yield only (ST1), for milk production efficiency only (ST2, with the ratio MILK / FBW as a criteria of production efficiency), or for milk yield, body condition and age (MT). Starting values were the result of a stabilizing period of random culling during 20 years before the 40 years shown during which selection strategies were applied.

The comparison between unselected and selected genotypes in Table 1 shows that the selection scenario modeled in a constant and favorable environment had only modest impact on the plasticity for the resource allocation to BR deposition (SATd) and to lactation (SATl). The greatest changes were observed for genotypes selected for production efficiency (ST2). In the case of nutritional limitation, it is expected that these animals would place less emphasis on defending their BR and more emphasis on their lactation than other genotypes.

Table 1: Average phenotypic values (standard deviation) of the partly heritable parameters of resource allocation for unselected herds and for selected herds obtained after 40 years of selection for milk yield only (ST1), for milk production efficiency only (ST2), or for milk yield, body condition and age (MT).

	Selection strategy			
Parameter[1]	Unselected herd (year 0)	ST1 (year 40)	ST2 (year 40)	MT (year 40)
d_0	0.27^a (0.045)	0.15^b (0.028)	0.17^c (0.032)	0.23^d (0.038)
l_0	0.74^a (0.054)	0.82^b (0.044)	0.86^c (0.031)	0.78^d (0.043)
SATd	0.50^a (0.050)	0.49^a (0.050)	0.51^a (0.050)	0.50^a (0.050)
SATl	0.50^a (0.051)	0.48^b (0.049)	0.47^b (0.049)	0.48^b (0.048)

[1] Parameters are basic components of the genetically driven allocation for body reserves deposition (d_0) and lactation (l_0), and parameters of environmentally driven modifications of allocation for body reserves deposition (SATd) and lactation (SATl) (See Animal Sub-model Description for further explanation)

[a-d] Within a row, means without a common superscript differ ($P < 0.05$)

Selection Consequences on Trade-Offs

The consequences of selection in a favorable environment in terms of progress for MILK relative to average survival and reproduction rates at the herd level are summarized in Fig. 7 (left panels). As indicated previously (Fig. 5) and shown with the ST1 trajectory, selecting for milk alone did not compromise survival as long as progress in resource acquisition was unlimited (i.e. a “win-win” situation). Conversely, when some limitation is imposed on body size increase by selecting for milk production efficiency there was a decrease in survival rate (ST2). However, the strongest side-effect of selection was observed on reproduction rate. Given the way the conception likelihood is determined in this model (i.e. a function of BCS level and BR balance), this trade-off between production and reproduction was consistent with the trends previously observed for MY and BCS (Fig. 6). Finally, none of the 3 different strategies was able to achieve milk yield progress without impairing to some extent survival or reproduction, or both.

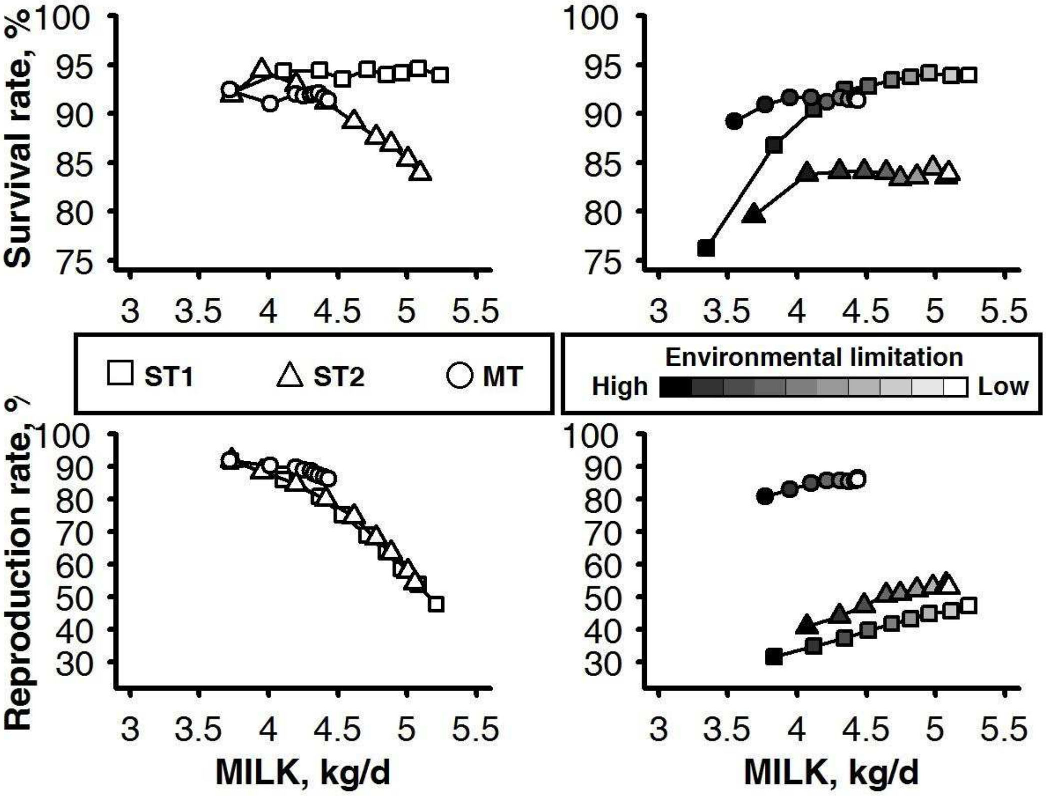


Figure 7: Left panels: trajectories of herd survival rate and reproduction rate relatively to average progress in milk yield at peak lactation during 40 years of selection in a favorable environment (unshaded symbols with each rightward progression reflecting 4 years of selection). Selection is for milk yield only (ST1), for milk production efficiency only (ST2), or for milk yield, body condition and age (MT). Right panels: at year 41, the instant effects of transferring selected herds obtained in year 40 to a range of progressively lower resource availability in the environment (shaded symbols where the darker the shading, the greater the environmental limitation imposed).

When the different herds selected for 40 years in a favorable environment were transferred to a range of environments with progressively more limited quantity of resources available (right panels), average MILK, survival and reproduction rates were decreased to a different extent. The different genotypes resulting from the 3 strategies thus differed in their sensitivity to the level of resource provided by the environment. However, no substantial differences were observed between plasticity parameters SATd and SATl of selected and unselected herds (Table 1), therefore the differences of environmental sensitivity were mostly expressed through the greater consequence of environmental limitations for animals with a high R_G, and thus larger body size (ST1), rather than through a genetic basis of allocation plasticity.

DISCUSSION

The aim of this study was to contribute insight into the development of associations between traits within a herd, as a consequence of both an animal's resource allocation across its lifetime, and the selection for one or more different performance outcomes by the manager. This required the construction and integration of 3 key features into a nutritional model: 1) incorporation of causal, partly heritable parameters, 2) sensitivity to both the selection strategy and the level of resource provided by the environment, and 3) variability in resource partitioning between animals, and within an animal across its lifetime.

Modeling Choices and Design

It is important to point out some of the modeling choices taken will have influenced the simulation results. Notably, it has been demonstrated that in a resource allocation model, the allocation hierarchy as well as the genetic variation assumed at each level affect the direction and the rate of the selection response (Worley et al., 2003). The reason for this is that genetic progress is expected to be faster in directions with ample genetic variation. Simple quantitative genetic models have been used to investigate these aspects (van Noordwijk and de Jong, 1986; Worley et al., 2003; Malausa et al., 2005). However, these models do not incorporate the dynamic nature of resource allocation and body reserves within an animal's lifespan, nor allocation adjustments according to feedback from environmental stimuli. These aspects were incorporated here, as they impact upon phenotypic performances and thus on the ranking of animals when the manager is selecting herd replacements and breeding males. The within lifespan effects also impact on probability of survival and probability of reproducing. Incorporation of these features in the model constrained the choices made, including that of using a given allocation hierarchy. Others choices of hierarchy may be possible and it would be useful to test their theoretical implications, especially if the model was to be further developed for the purpose of on-farm prediction.

A central point of the model design was to distinguish the resource acquisition from its subsequent allocation which is different from most nutritional models that generally blend these 2 notions into the notion of potential performance (Emmans and Kyriazakis, 2001). The theoretical basis for this distinction is the possibility for individual variation in resource acquisition (phenotypic or genetic or both) to be independent of variations in allocation (van Noordwijk and de Jong, 1986). In our model, this was represented by assuming that variation in potential resource acquisition (R_G) observed at one time of life would be essentially a consequence of previous allocation decisions reflected in actual body size (BWnl) and fatness (BCS). Thus no explicit and independent genetic control in resource acquisition was assumed (e.g. by setting parameter ‘a’ in R_{G0} as heritable). A high R_G (i.e. high BWnl and low BCS) implies not only benefits (by increased resource acquisition) but also increased energetic costs of maintenance related to animal size. Although there is strong evidence for the relationship between body size, fatness and intake (Tolkamp et al., 2007), the representation of this in the present model is most likely an oversimplification relative to the biological complexity behind the resource acquisition process. Such underlying biology may also interact with environmental cues such as season (Rhind et al., 2002), and drive other variations in the resource acquisition (even on a time-step of week). However, an important issue for models of resource allocation is to simply represent the integration of the acquisition process and the constraints on its evolution (Boggs, 1992), which often requires identifying fitness costs of intake (Illius et al., 2002; Yearsley et al., 2005). Most of the resource allocation models have been developed in the context of wild animals, without explicitly integrating a process of resource acquisition because the resource obtained is often simply assumed to be limited by the environment. In contrast, the development of resource allocation models for the farm-context, i.e. with a more controlled environment, may strengthen the necessity to consider this issue. The model presented here provides a basis for such consideration.

Incorporation of Causal Genetic Parameters

From the viewpoint of nutrient partitioning, studying the consequences of a particular selection strategy and for a particular herd situation is a major issue to better understand the basis of individual differences and make useful predictions for both selecting and managing high yielding animals (Friggens and Newbold, 2007). The approach proposed in this study was to consider that selection at the level of the observed phenotype is acting on genetic parameters from an underlying biological level of resource allocation rather than on a potential phenotype or potential of performance, as is generally assumed in nutritional models (Emmans and Kyriazakis, 2001; Bryant et al., 2005). Although selection is practiced at the level of the observed phenotype there are no genetic parameters for performance levels per se. As these allocation parameters represent costs and benefits in terms of animal survival and reproductive performance, the combinations of parameters that arose were those of individuals that were both viable in terms of reproductive fitness and survival, while also fitting the alternative breeding objectives used to drive the selection strategies. This model property offered the appealing possibility to incorporate genetic parameters without any statistical correlation a priori. In other words, part of the genetic correlations classically assumed between performances was already implicitly built-in to the model at the level of resource allocation. Others studies have considered the incorporation of genetic parameters at an underlying biological level, for instance for lactation (Bryant et al., 2007) or growth (Doeschl-Wilson et al., 2007), but this may well be the first approach in animal breeding and nutrition which applies to a whole set of life-functions. The model has been developed as a proof of principle with the intention of taking a step further relative to the insightful model of Van Der Waaij (2004) in which animals allocate a resource between 2 stylized functions (termed “production” and “fitness”), and on a time-step of a generation.

Sensitivity to Selection and to the Environment

Long-term selection responses in a constant environment illustrated the model sensitivity to different selection strategies. Although, similar selection responses may be observed for contrasting selection objectives (ST1 and ST2 both led to a steady increase in milk yield associated with an opposite trend for BCS), it may rely on different changes in resource allocation that reveal differences in environmental sensitivity.

Selection for milk production in ST1 led to larger animals so that most of the progress in milk yield was achieved by a correlated increase in resource acquisition, without impairing survival. This selection response is consistent with selection between breeds of small ruminants such as sheep, where larger breeds tend to do best in more intensive systems with high level of concentrate feeding (Dickerson, 1978). Conversely, when some limitation is imposed on body size increase as part of the selection criteria, the progress in milk yield was more directly due to a change in partition towards lactation when compared with selecting for milk production alone. The result of this was that survival was impaired. A quick scan of breeding objectives will indentify many instances of a downward penalty on mature size. Overall, the results here for the 2 single–trait selection strategies converge with those of Van Der Waaij (2004). In all cases, it seems that the emergence of a trade-off between survival and production during selection depends on whether or not a correlated increase in resource acquisition can compensate for a high selection pressure on resource allocation. Our results indicate that a trade-off between reproduction and milk production emerged regardless of the criteria used in single-trait selection. This was because the conception likelihood was strongly influenced by the level of BCS (Friggens and Chagunda, 2005), which showed a decreasing trend during selection.

The 3 selection strategies developed different sensitivities to a common decrease in resource availability and this can reflect different risk attitudes between managers in commercial herd situations. When animals were not only selected for milk but also for fitness related traits, i.e.

body condition and age (MT), milk progress was slower than for single-trait strategies and trade-offs with survival and reproduction did not emerge so strongly. Moreover, females from the MT strategy were less exposed to nutritional shortage through their greater BCS after selection which resulted in a high and robust survival rate. This multi-trait selection response may thus reflect the preference of risk-averse managers to find robust solutions to keep rates of involuntary culling and rates of reproductive failures low across years rather than solutions aiming at purely maximizing the progress in milk yield or production efficiency (Robertson, 1966), as it was the case for single trait strategies. Indeed, large females from ST1 strategy had the greatest potential for resource acquisition and this offered the greatest opportunity to achieve milk yield progress as long as a good nutritional environment can be provided. However, these large females had to pay for a high cost of maintenance to maintain their probability of survival. As, they did not develop neither a plasticity to reallocate their resource obtained towards survival nor body reserves to mobilize, they were globally more sensitive in terms of survival. This agrees with observations in dairy herds with high intensity of production (Windig et al., 2005) which have been found to get lower somatic cell count (SCC) on average but a high risk of involuntary culling for the high producing cows (which is congruent with ST1 when SCC is taken as a proxy for coping ability and indirectly survival).

In terms of reproduction, the herds following the 3 different simulated selection strategies responded similarly by a linear decrease with increasing milk yield whereas survival was initially maintained before collapsing. Globally, such a response is thus consistent with the conservative tactic of energy allocation characteristics of long-lived animals like goats, i.e. survival is prioritized over reproduction (Hamel et al., 2011). However the lack of clear differences in the reproduction response to increasingly limited environments between single-trait strategies and the MT strategy is surprising because it would be expected that when a lot of females come close to the risk of dying (like in ST1), investment into future reproduction would be suddenly shut down. Further consideration of functional forms within the model and their parameterization would be required to address more complex prioritization of survival over reproduction under severely limiting environments

Variability between Animals and within an Animal across its Lifetime

In the present study, the expression of individual variability was voluntarily restricted because the simulation experiments were primarily run to provide proofs-of-principle for the proposed approach, i.e. the incorporation of a genetic basis into a nutritional model. Thus, time-variations in the level of resource provided by the environment and individual-variations in physiological stage due to the reproductive management were not simulated. However, these components of individual variability have been shown to structure the diversity of lifetime performance both inter-management and intra-management (Puillet et al., 2011; Tichit et al., 2011). Interestingly, different management options can lead to similar levels of feed efficiency at the herd level while relying on different contrasts of biological capabilities at the level of individuals. In this simulation approach, the biological capabilities are the driving forces of individual variability relative to a mean herd production potential. Proposing another individually-based representation with its own heritable parameters offers a way to extend such an analysis by incorporating genetic effects and their interactions with a particular herd environment (G × E). It is our belief that in the future, our approach can help to investigate intriguing questions for both nutritionist and geneticists, such as, the extent to which phenotypic and genetic correlations between traits can be changed by herd management (Calus et al., 2005).

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APPENDICES

Animal Sub-Model Equations

Variable	**Equation**
Status	
LIV (t)	= 1 if living, 0 else
LACT (t)	= 1 if lactating, 0 else
PREG (t)	= 1 if pregnant, 0 else
BRpart	= BR value when tlact = 1
BWpart	= BW value when tlact = 1
Time variables	
age (t)	= age (t-1) + LIV (t)
tlact (t)	= tlact (t-1) + LACT (t)
tpreg (t)	= tpreg (t-1) + PREG (t)
Resource acquisition	
Resource obtaining from the environment:	
R_{G0} (age)	$= a \times BWnl\ (age-1) + R_GOff$
R_GOff	$= aoff \times BWoff$
BWoff	$= (1 - exp(-kBWoff \times tlact)) \times BWpart \times weaning$
weaning	$= exp(-kwean \times tlact)$
R_G	$= R_{G0} \times (1 - b \times (BCS - BCS^*))$
$Robt_E$	$= min(R_G \times Q_E, R_E)$
SAT	$= Robt_E / R_{G0}$
Resource obtaining from body reserves mobilization:	
$Rmob_G$	$= amob_G \times BRpart \times exp(- kmob_G \times tlact)$
$Rmob_E$	$= amob_E \times BWnl \times (1 / (1 + exp(- Rat_{mobE} \times (SAT - SAT_{mob})))$
- Total resource obtaining:	
Robt	$= Robt_E + Rmob_E + Rmob_G$
Resource allocation (following the model $c = c_0 \times cmod_G \times cmod_E$)	
Genetically driven modification (cmodG)	
dmod	$= 1 - exp(- kdep \times tlact) \times LACT$
pmod	$= (tpreg / Lpreg)^4$
lmod	$= exp(- klact \times tlact)$
gmod	$= exp(- kgrow \times age)$
Environmentally driven modification ($cmod_E$)	
$cmod_E$	$= 1 / (1 + exp(- Rat_{cmodE} \times (SAT - SATc_0))$
Resources allocated	
Rdep	$= d \times Robt$
Rpreg	$= (1 - d) \times p \times Robt$
Rlact	$= (1 - d) \times (1 - p) \times l \times Robt$
Rgrow	$= (1 - d) \times (1 - p) \times (1 - l) \times g \times Robt$
Rsurv	$= (1 - d) \times (1 - p) \times (1 - l) \times (1 - g) \times Robt$
Rpreg_foet	$= u_0 \times Rpreg$
Rpreg_dep	$= (1 - u_0) \times Rpreg$
Resource conversion	
dBR	$= dt \times ((Rdep + Rpreg\_dep) / E_{BRdep} - (Rmob_E + Rmob_G) / E_{BRmob})$
dGU	$= dt \times Rdep\_foet / E_{GU}$
MYcor	$= dt \times Rlact / E_{MYcor}$
dBWnl	$= dt \times Rgrow / E_{BWnl}$
BR (age)	= BR (age-1) + dBR
GU (tpreg)	= GU (age-1) + dGU
BWnl (age)	= BWnl (age-1) + dBWnl
SURV	$= (1 / (1 + exp(- Rat_{SURV} \times (Rsurv^* - Rsurv_0))) \times exp(- kage \times age)$
$Rsurv_{st}$	$= Rsurv / (BWnl + X_{BWoff} \times BWoff)^{0.75}$
CONC	$= 1 / (1 + exp(- Rat_{CONC} \times (BCS - (BCS_0 - BCSmod))$

BCSmod	= X_{BR} × dBR
Empirical transformations	
BCS	= 10 × BR / (BWnl + BR)
FBW	= (BWnl + BR) / 0.817
DMI	= $Robt_E$ / 10.2

Biological constants

Name	**Value**	**Units**	**Description**
Resource acquisition:			
Parameters of resource obtaining from the environment (RobtE)			
a	0.9	MJ/kg	Unitary potential of acquisition (per kg of BWnl)
aoff	0.81	MJ/kg	Unitary potential of acquisition (per kg of BWoff)
kBWoff	0.1	wks^{-1}	Decay constant used for a reference offspring growth
kwean	0.07	wks^{-1}	Decay constant used for a reference offspring weaning
b	0.09	MJ/pts	Scaling factor for BCS feedback on acquisition
BCS*	2.5	pts	Target BCS
Parameters of resource mobilization (Rmob)			
$amob_G$	0.23	MJ/kg	Unitary potential of mobilization RmobG (per kg of BWpart)
$kmob_G$	0.2	wks^{-1}	Decay constant used for RmobG
Rat_{mobE}	15	uniteless	Rate for RmobE
SAT_{mob}	0.4	uniteless	Basic level of SAT for RmobE
$amob_E$	0.3	MJ/kg	Unitary potential of mobilization RmobE (per kg of BWnl)
Resource allocation:			
Basic components of the genetically driven allocation (c_0)			
p_0	0.5	uniteless	for pregnancy allocation
g_0	0.5	uniteless	for growth allocation
u_0	0.7	uniteless	part of Rpreg allocated to the gravid uterus for foetal development (remaining part 1 – u_0 allocated to BR)
<u>Note</u>: genetic variation was implemented for basic allocation components of BR deposition (d_0) and lactation (l_0)			
Parameters of the genetically driven time-modifications of allocation ($cmod_G$)			
kdep	0.01	wks^{-1}	Decay constant used for pregnancy allocation
klact	0.02	wks^{-1}	Decay constant used for lactation allocation
kgrow	0.027	wks^{-1}	Decay constant used for growth allocation
Lpreg	22	wks	Length of pregnancy
Parameters $SATc_0$ of environmentally driven modifications of allocation ($cmod_E$)			
SATp	0	uniteless	Basic $SATc_0$ for pregnancy allocation
SATg	0.5	uniteless	Basic $SATc_0$ for growth allocation
Rat_{cmodE}	15	uniteless	Rate for $cmod_E$
<u>Note</u>: Genetic variation was implemented in components $SATc_0$ for reserve deposition (SATd) and lactation (SATl)			
Resource conversion			
Metabolizable energy conversion factors			
E_{BRdep}	46.3	MJ/kg	for BR deposition
E_{BRmob}	25.5	MJ/kg	for BR mobilization
E_{GU}	29	MJ/kg	for fetal development
E_{MYcor}	4.57	MJ/kg	for energy corrected milk production
E_{BWnl}	27	MJ/kg	for non-labile growth
Parameters of survival (SURV) and conception (CONC) likelihoods			
Rat_{SURV}	15	kg$^{0.75}$/MJ^{-1}	Rate for SURV likelihood
$Rsurv_0$	0	MJ/kg$^{0.75}$	Basic level of Rsurv used in SURV
kage	1.9×10^{-5}	wks^{-1}	Decay constant used for survival decrease with age
X_{BWoff}	1	kg/kg	Scaling factor for BWoff effect on SURV
Rat_{CONC}	2	pts^{-1}	Rate for CONC likelihood

BCS_0 X_{BR}	2 1	pts pts/kg	Basic level of BCS used in CONC Scaling factor for dBR effect on CONC
dt	7	d	Time step used

Simulation of genetic variation and inheritance

In the base population of parents, the phenotypic value P_i of a trait *i* (d_0, l_0, SATd and SATl) was expressed as follows:

$$P_i = \mu_{Pi} + TBV_i + \varepsilon_i \,,$$

where μ_{Pi} is the phenotypic population mean of trait *i*, TBV_i is its true breeding and ε_i is a simulated random environmental effect. These terms were defined from the trait heritability ($h^2{}_i$) and its phenotypic standard deviation (σ_{Pi}), as follows:

$$TBV_i = \delta_1 \times \sqrt{h^2{}_i} \times \sqrt{\sigma_{Pi}{}^2}\text{, and } \varepsilon_i = \delta_2 \times \sqrt{(1-h^2{}_i)} \times \sqrt{\sigma_{Pi}{}^2}\,,$$

where δ_1 and δ_2 are random deviates sampled from a normal distribution (with a mean of zero and a standard deviation of 1).

To respect the constraint on trait d_0 and l_0 (i.e. they must be between 0 and 1), the phenotypic value P_i of these traits was transformed (P_{Ti}) with a logistic function as follows:

$$P_{Ti} = \frac{1}{1 + \exp(-4 \times (P_i - 0.5))}$$

In this equation, the values of the rate (−4) and of the decay (0.5) allows P_i to be relatively unaffected by the transformation ($P_{Ti} \approx P_i$) when P_i values are close to 0.5. When P_i becomes lower than 0.5 P_{Ti} converges toward 0 and when P_i becomes greater than 0.5 P_{Ti} converges toward 1.

Once the model has been initialized with a base population of parents, TBV_i of new offspring individuals (TBVo) are simulated as a function of male (TBVm) and female (TBVf) parent TBVs and a Mendelian sampling term as follows:

$$TBVo = 0.5 \times (TBVm + TBVf\,) + \sqrt{0.5} \times \delta \times \sqrt{h^2{}_i} \times \sqrt{\sigma_{Pi}{}^2}\,,$$

where δ is a random deviate sampled from a normal distribution (with a mean of zero and a standard deviation of 1). Inbreeding was not considered here.

Paper 2

Characterization of a changing relationship between milk production and live weight for dairy goats undergoing extended lactation

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ABSTRACT

This study aimed to characterize the time-profile of extended lactation (EL) for dairy goats, and the relationships between milk production, live weight and intake that are associated with this profile. For this, 20 non-pregnant multiparous dairy goats were monitored daily for about 90 d from the onset of EL, i.e. when an increase in milk yield (MY) was observed. These 20 individual profiles were pooled to create a group average profile at the onset of EL for the purpose of parameterizing a simple compartmental model. Moreover, 9 of the 20 EL-goats have been kept to compare their 24-mo profiles of body weight (BW) and milk production with those observed during two successive “normal lactations” (NL). Despite being kept in the same environment and on the same feed, a clear change from decreasing to increasing MY was identified (T_{change}) for all of the 20 EL-goats around 330 d in milk (DIM). During the whole 24 mo-period, EL-goats produced as much milk as NL-goats but this total milk production was unequally split before (56 %) and after (44 %) T_{change}. In terms of BW, the most striking difference between EL and NL goats was the rapid and very high increase (+ 9.3 kg with an ADG of 60.4 g/d) that was observed concurrently with the increase of MY. Model parameterization with the group average profile does not support that the rise in MY drives the increase in resource acquisition as is generally assumed at the onset of a NL. Rather, it demonstrates the transfer of energy from feed to milk is delayed at the onset of EL. Moreover, assessing the model ability to fit the range of individual profiles showed that the performances over the first 90 d of EL are largely predetermined by the animal state at T_{change}. The analysis of individual variability in EL efficiency showed that it depends both on an increase in resource acquisition and on the potential of goats to partition energy from the diet towards milk production instead of to body tissue gain. Finally, predicting the suitability for EL requires the consideration of more than just milk production for 300 DIM.

Key Words: dairy goat, extended lactation, modeling

INTRODUCTION

Extending the lactation of dairy females beyond 300-d is increasingly considered in the management strategies of cow and goat systems. The practical implications at the herd level have been explored (Butler et al., 2010; Rotz et al., 2005). However, these approaches are often confronted with a multiplicity of factors that potentially affect the efficiency of an extended lactation in a particular situation. This is especially the case for pasture fed dairy cows where complex effects on production have been put forward as a result of different combinations of season, diet and breed (Kolver et al., 2007; Grainger et al., 2009; Butler et al., 2010). These findings have stimulated interest in finding generic characteristics of extended lactations that could be used across different nutritional contexts in dairy systems (Dematawewa et al., 2007; Steri et al., 2012).

Despite qualitative similarities between the standard 300-d lactation of dairy cows and goats, there is some evidence that goats represent a particular case of extended lactation. In the dairy cow, it is frequently reported that, even under non-limiting nutritional conditions, milk yield continuously declines after the normal 300-d period (Grainger et al., 2009). There are very few reports describing extended lactation in goats but in all of them, it seems that the onset of extended lactation could be defined by an increase of milk yield (Salama et al., 2005; Chastin et al., 2001). In these 2-yrs studies, extended lactation did not lead to significant loss in milk yield compared with two lactations of 300-d with a 12-mo kidding interval. Moreover, it has been observed that well-fed dairy goats can extend their lactation to last from 2 to 4-yr by increasing seasonally their milk secretion although there was an overarching trend for milk yield to decline (Linzell, 1973a). In this latter study, the seasonal fluctuations in milk yield throughout the lactation suggested that mammary function is not only affected by nutrition but that there is an underlying, innate, biological mechanism involved beyond 300-d of lactation. This raises the question, as yet unexplored, of which animal factors influence this onset of extended lactation.

Together with the description of Salama et al. (2005), these results indicate the need for a better characterization of extended lactation profiles in the dairy goat not just in terms of milk yield but also in terms of being able to model the performance parameters linked to nutrient partitioning. Accordingly, the present study aims to characterize the time-profile of extended lactation for dairy goats, and the relationships between milk production, live weight and intake that are associated with this profile. Particular focus will be given to the period when lactation is normally initiated, which is usually a critical period in dairy goats. A second aim was to model these changes so as to shed light on the animal factors influencing their shape.

MATERIALS AND METHODS

Animals and Housing

Twenty multiparous dairy goats (6 Saanen and 14 Alpine) were selected from the experimental herd of Grignon. After kidding in January 2009, these goats were not rebred 7-mo later as would usually be the case for goats with a 12-mo kidding interval in a "normal lactation" (NL). The 2-mo dry period was omitted for the goats in extended lactation (EL), which continued to be milked twice a day. This group was monitored in individual pens from December 21st, 2010 to March 7th, 2011 in order to characterize performance at the onset of EL (from about mo 11 to 14 of lactation). Beyond March, 2011, 9 of the 20 goats have been kept to compare 24-mo EL profiles (the 24-mo kidding interval including 22 mo of lactation) with NL profiles that were selected a posteriori on the basis of similar BW and MY from 0 to 300 DIM. During their EL, goats were fed the same TMR diet as the other goats from the herd. The TMR consisted of grass hay (250 g/kg DM), alfalfa (240 g/kg DM), sugar beet pulp (300 g/kg DM), brewer's grain (50 g/kg DM) and concentrate blend (160 g/kg DM). The concentrate blend consisted of 25% wheat, 25% barley, 30% maize, 15% soybean meal, 3% molasses, and 2% mineral premix composed of 18% P, 14% Ca and 6% Mg. Energy and protein values of the diet were calculated according to the INRA tables (Baumont et al., 2007). PDIN (i.e. true protein digested in the small intestine when fermentable N is limiting) was 84.4 g/kg DM and PDIE (i.e. true protein digested in the small intestine when fermentable energy is limiting) was 83 g/kg DM. The net energy content of the diet (E_{diet}) was 6.12 MJ/kg DM (the INRA system uses a single energy unit for all physiological functions, i.e. the same efficiency is assumed for the conversion of metabolizable energy to net energy). The quantities offered were adjusted weekly to achieve 10% refusals.

Biometric Approach for Characterizing Extended Lactations with the 24-mo Profiles

Measurements. The profiles of performances of EL and NL were characterized with the data from routine herd monitoring. This was done weekly and included for each goat the average daily milk yield (MY) and a body weight measure (BW). Milk composition (fat and protein) and somatic cell count (SCC) were recorded monthly and are also reported in this study.

Performance Matching Procedure. To get comparable profiles between EL and NL, the MY and BW curves prior to the onset of EL, i.e. from conception to wk 30 of lactation were visually examined. For each EL, the NL candidate whose curves best matched was retained to form a pair. As far as possible, the 9 pairs were formed using NL data from 2010 and 2011. However, due to the requirements for the matching procedure some NL profiles were chosen among data recorded from previous years.

Time Alignment of EL and the Second Lactation of NL. Visual inspection of the EL curves showed a rise in MY at about 330 DIM that could correspond to a physiological change. To detect more precisely when this change occurred for the different goats, a 3rd degree polynomial of MY on DIM was fitted for each EL animal in the period 300 to 390 DIM. The time of change (T_{change}) was defined as occurring when estimated MY was at a minimum in the considered period, i.e. when the first derivative equals zero.

For comparison with NL, each of the 24-mo EL profiles was split at T_{change}. The second part of EL-profiles describing the performances from T_{change} to drying-off was then time-aligned and compared with the second lactation of NL.

Statistical Analyses. Data were analyzed with a mixed model that contained the fixed effects of week of lactation (month of lactation for milk composition and SCC), the interaction between week of lactation and the treatment (NL or EL), the random effect of the pair (1 to 9) and the residual error. Analysis was performed with the lmer function from the lme4 package in the R-environment (version 2.15.1, R Development Core Team, 2012).

Study of the Onset of Extended Lactation

Measurements. For the 20 EL goats, MY, BW and dry matter intake (DMI) were recorded daily for 11 weeks, starting from December 21st, 2010. During this period, goats were kept in 2 m × 1 m individual pens to monitor DMI. DMI was calculated from the difference between the quantity offered and the refusals that were removed and measured every day at 1400 h. Milk composition (fat and protein contents) was recorded every 3 days. Energy balance (EB) was calculated according to the formula published by Sauvant et al., (2007). Details of the calculation are reported in Appendix. The onset of each of the 20 EL was considered as a 90 d period starting at T_{change} (detected as before). On average T_{change} occurred 11.5 d (SD = 10.3) before the start of the daily monitoring procedure. To compensate for the lack of data during the first days after T_{change}, BW and MY records were partially completed with those from the weekly routine monitoring. The individual profiles obtained at the onset of EL were pooled to create a group average profile for the purpose of parameterizing a simple compartmental model. The model was built using ModelMaker (version 3, Cherwell Scientific Ltd., Oxford, UK) to fit simultaneously the evolution of DMI, MY, milk composition and BW at the onset of EL. The model parameters were also estimated using ModelMaker software. For clarity, the model rationale and its main equations are described together with the modeling results. Further details about the model equations are presented in the Appendix.

Statistical Analyses. The Root Mean Square Error (RMSE) was used to evaluate the quality of the model to fit the observed data. Using the group average profile, for each variable, RMSE was defined as follows:

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{N}(O_i - P_i)^2}{N}}$$

where O_i is the ith observed value, P_i is the ith predicted value and N is the total number of observations. A coefficient of determination (CD) was also calculated to quantify the ability of the model to explain the observed variability in the data.

To assess the model ability to fit the range of individual profiles (n = 20) the model was run with the initial parameters (DMI_0, MY_0, Fat_0, $Protein_0$, and BW_0) adjusted to each individuals but keeping the others parameters fixed to group average profile values (Appendix; Table 1). The individual adjustments were evaluated globally with a CD quantifying the proportion of the intra individual variability for each variable (CD_{RES}). CD_{RES} was defined as follows:

$$CD_{RES} = 1 - \frac{\sum_{k=1}^{n}\sum_{j=1}^{n_k}(O_{j,k} - P_{j,k})^2}{RSS}, \qquad \text{with } RSS = \sum_{k=1}^{n}\sum_{j=1}^{n_k}(O_{j,k} - \overline{O}_k)^2$$

where $O_{j,k}$ and $P_{j,k}$ are respectively the jth observation and prediction for the kth individual (n = 20 individuals) and RSS is the residual sum of squares calculated with the mean of the n_k observed data from the kth individual ($\overline{O}_k$).

The relations between model parameters and goat performances during EL were explored with principal component analysis (PCA). The similarities between individuals were investigated with hierarchical clustering on principal components (HCPC) using the Ward criterion of information. All the exploratory data analysis was performed with R and the FactoMineR package (version 1.19, 2012).

RESULTS

Despite being kept in the same environment and on the same feed, a clear change from decreasing to increasing MY was identified (T_{change}) for all of the 20 EL goats around 330 DIM (MEAN ± SD = 333 ± 18.3 DIM). This occurred between November 20th, 2010 and December 24th, 2010 without any obvious relation with the date of previous kidding.

Comparison of Extended Lactation with the 24-mo Profile of Two Successive Normal Lactations

The comparison of average daily MY and BW are presented in Figure 1. The first lactation period in EL goats (labeled "n-1") was similar to the equivalent lactation of NL and was thus considered as a basis for further comparison between EL and NL. During this period, significant differences ($P < 0.05$) in MY and BW occurred from wk 37 onward at which time NL goats were 7 wks pregnant. The average BW of EL goats showed almost no increase from wk 37 to T_{change} even though there was not a pregnancy associated increase in energy requirements during this time and the requirements for milk were decreasing as indicated by the decline in MY.

From the second period (labeled "n") beginning at T_{change} the average MY of EL goats increased for about 23 wks and peaked at 3.7 kg/d, that is about only 85% of the peak observed in period n-1 (Figure 1A). A substantial increase of BW was also observed at the same time (Figure 1B). The EL profiles in the first 23 wks of period n are markedly different from NL because MY increased much more gradually after T_{change} than after kidding but for a period about three times longer than NL (peak at wk 10 of lactation). Moreover, as seen for NL goats, a phase of increasing MY is normally associated with body fat mobilization and consequently with BW loss whereas EL goats exhibited high ADG (average = 60.4 ± 9.4 g/d) during the first 23 wks of the period n. After these 23 wks, MY declined until drying-off$_n$ and BW remained globally steady (slightly decreasing) until wk 38. Mating occurred at wk 35 and BW increased about 6 wks after due to pregnancy, similarly to NL. The average BW by the end of pregnancy was equivalent for EL and NL. Thus, from wk 23 of period n, EL goats recovered BW and MY dynamics patterns similar to those of NL goats. During the whole 24 mo-period, EL goats produced as much milk (2192 ± 68 kg/goat) as NL (2193 ± 85 kg/goat) but contrarily to NL, this EL milk production was unequally split between period n-1 (56 %) and n (44 %). No significant differences were detected in milk fat and protein contents and in somatic cell counts (SCC) between EL and NL goats (Figure 2).

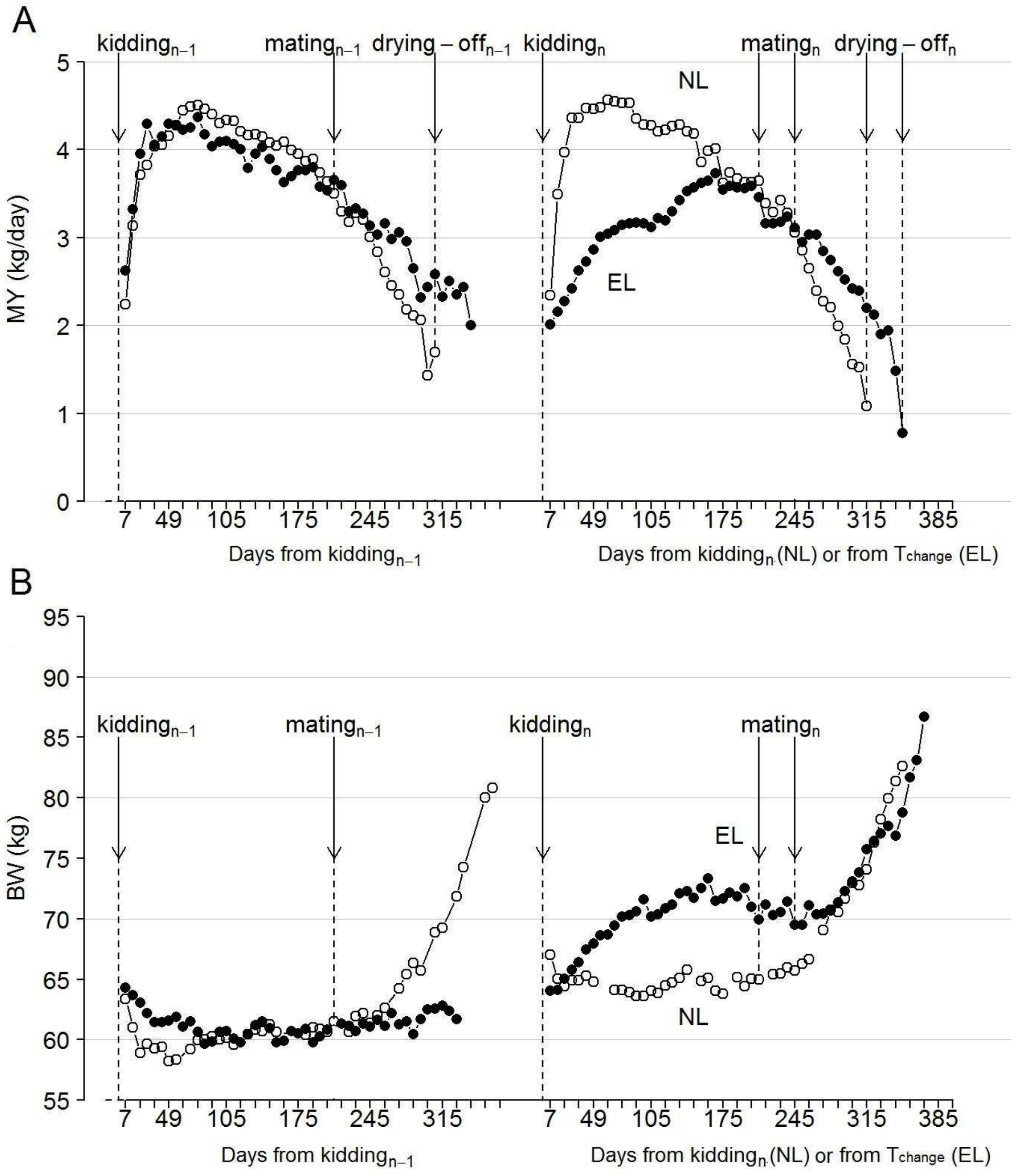

Figure 1. A) The average milk yield (MY) and B) body weight (BW) of dairy goats in extended lactations (EL: ●, n=9) and "normal lactations" (NL: ○, n=9). Period "n-1" denotes the first lactation in the study for NL goats and the equivalent period for EL goats. Period n denotes the second lactation for NL goats and the time-aligned extended lactation of EL goats. The time point used to split the extended lactation into periods n-1 and n called T$_{change}$ was the point at which MY started to rise again (See Material and Methods for further explanation).

Given that the substantial differences between EL and NL profiles occurring at the same time, under the same feeding conditions, and in the same environment, it seems clear that there is another driver of nutrient partition and milk production than feed quality and DIM. As a means to explore this, we adopted a modeling approach to the EL data.

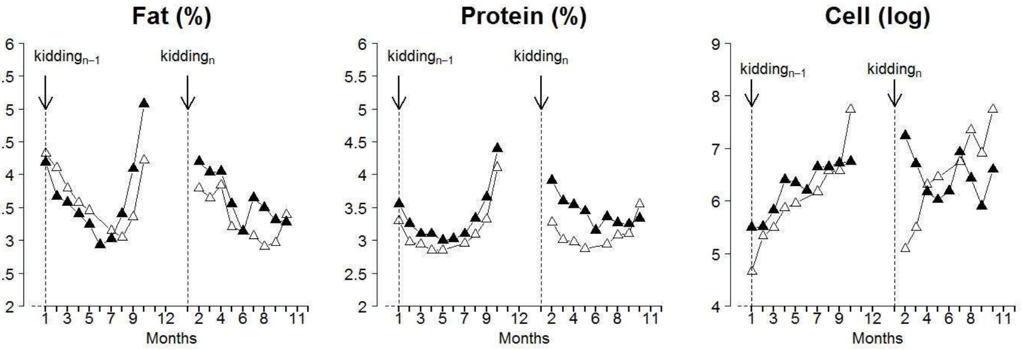

Figure 2. Average milk fat, protein and SCC for EL (▲, n=9) and NL (Δ, n=9). Periods "n-1" denotes the first lactation in the study for NL goats and the equivalent period for EL goats. Period n denotes the second lactation for NL goats and the time-aligned extended lactation of EL goats. The time point used to split the extended lactation into periods n-1 and n called T_{change} was the point at which MY started to rise again (See Material and Methods for further explanation).

Modeling the Group Average Profile at the Onset of the Extended Lactation

The purpose of this modeling work was to characterize the linkage between intake, milk production and BW and in particular the time lags between their dynamics as this provides information on which of these is driving the others. For this reason, the model does not attempt to describe specific physiological mechanisms.

In order to represent an overall dynamic at the onset of EL, the group average profile calculated from the 20 onset-EL profiles was used to parameterize the initial model. The profiles of 6 characterizing variables are presented in Figure 3A (DMI and MY), 3B (BW and EB) and 3C (milk fat and protein contents). During the 90 d of the onset-profile, DMI as well as MY seemed to increase according to a non linear trend over the 90 d (Figure 3A), although DMI appeared to increase faster to its asymptotic value than MY. BW seemed to increase linearly from about 65 to 72 kg (Figure 3B), with an ADG of about 80 g/d. However, relatively few measures of BW were available for the first 2 wks whereas there could be some increase in ADG at this moment. The increase in BW was consistent with the positive values of the calculated EB (mean value of + 3.03 ± 0.13 MJ/d). Mean milk fat and protein content decreased in a similar fashion although much more individual variation was observed for fat.

Figure 4 presents the diagram of the model used together with the main equations (further details are provided in Appendix). Parameter definitions are presented in Table 1. Model development was based on the approach proposed by Sauvant (1994), and previous applications of this approach (Desnoyers et al., 2009; Puillet et al., 2008). The basic principle consisted in building the simplest possible dynamic compartmental structure that allows time-lags between driving factors to be quantified.

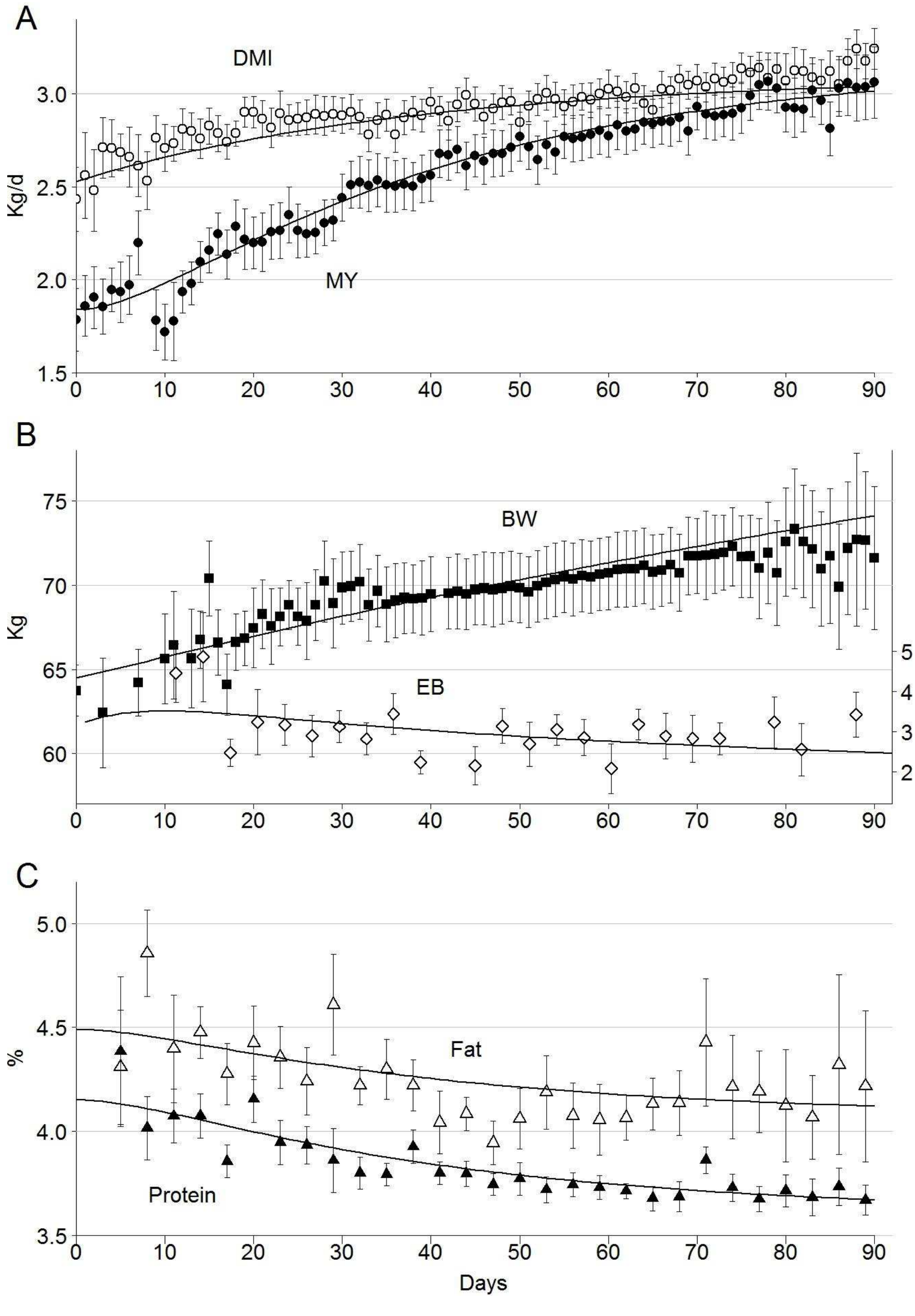

Figure 3. A) The average intake (DMI; ○), milk yield (MY; ●), B) body weight (BW; ■), energy balance (EB; ◊), and C) milk fat (Δ) and protein (▲) contents relative to the onset of extended lactations in dairy goats (daily mean values ± SE). The continuous line represents the fitted model.

In our case, this structure was built on the hypothesis of a global delay in the transfer of energy from feed to milk during the whole onset period of EL. The underlying dynamic was based on two successive first-order reactions: A→B→C where A, B and C are relative quantities of these linked driving factors that control the variables DMI, MY, Fat and Protein. The change with time of A, B and C is presented in Figure 5. The fractional outflow rates k_{AB} and k_{BC} are two key parameters used to characterize the global delay in energy transfer from feed to milk (Table 1). By controlling the discharge of compartment A into B, k_{AB} activates the rise in DMI (DMI is driven by (1 − A)). The mean residence time of A (defined by $1/k_{AB}$) is the time needed to increase the quantity (1 − A) from its initial value (0) to about 0.63 (Figure 5). In others words, k_{AB} controls the rate of increase in DMI and, as a consequence, the rate of increase in energy input. By controlling the discharge of compartment B into C, k_{BC} activates the changes in milk variables. MY increase is driven by C whereas fat and protein contents decreases are driven by –C. The mean residence time in compartment B (defined by $1/k_{BC}$) is the extra-time to $1/k_{AB}$ which is needed to increase the quantity C from its initial value (0) to about 0.63 (Figure 5). In others words, k_{BC} controls the time-lag between the rise in DMI and the changes in milk variables and, as a consequence, the time-lag between the changes in feed energy input and milk energy output. Any change in the driven variables DMI, MY, Fat and Protein result from the multiplication of the driving factors with 4 scaling parameters (Figure 4), the values of which were obtained by fitting to the average EL profile (α_{dmi}, α_{my}, α_{mf} and α_{mp} in Table 1). Initially (at T_{change} or d 0 of the EL-profile) the relative quantity of A is 1, i.e. 100%, so that of B and C is zero (Figure 5). As a consequence, none of the variables DMI, MY, Fat and Protein is influenced by the driving factors at d 0, so their value only equals the initial estimates (DMI_0, MY_0, Fat_0 and $Protein_0$).

Table 1. Definition of the parameters used in the model to predict a group average time profile of performances at the onset of extended lactation in dairy goat. See text and Appendix for further explanation

Parameter name	Units	Description	Value adjusted to the Average Profile (n=20)
k_{AB}	(1/d)	fractional outflow rate from A to B	0.026
k_{BC}	(1/d)	fractional outflow rate from B to C	0.134
α_{dmi}	none	scaling parameter between (B+C) and DMI value	0.563
α_{my}	none	scaling parameter between C and MY value	1.335
α_{mf}	none	scaling parameter between C and Fat value	0.419
α_{mp}	none	scaling parameter between C and Protein value	0.544
DMI_0	kg/d	value of DMI at time T_{change} of lactation	2.53
MY_0	kg/d	value of MY at time T_{change} of lactation	1.84
Fat_0	%	value of Fat at time T_{change} of lactation	4.49
$Protein_0$	%	value of Protein at time T_{change} of lactation	4.15
BW_0	kg	value of BW at time T_{change} of lactation	64.5
E_{diet}	MJ/kg	net energy of the diet	6.12

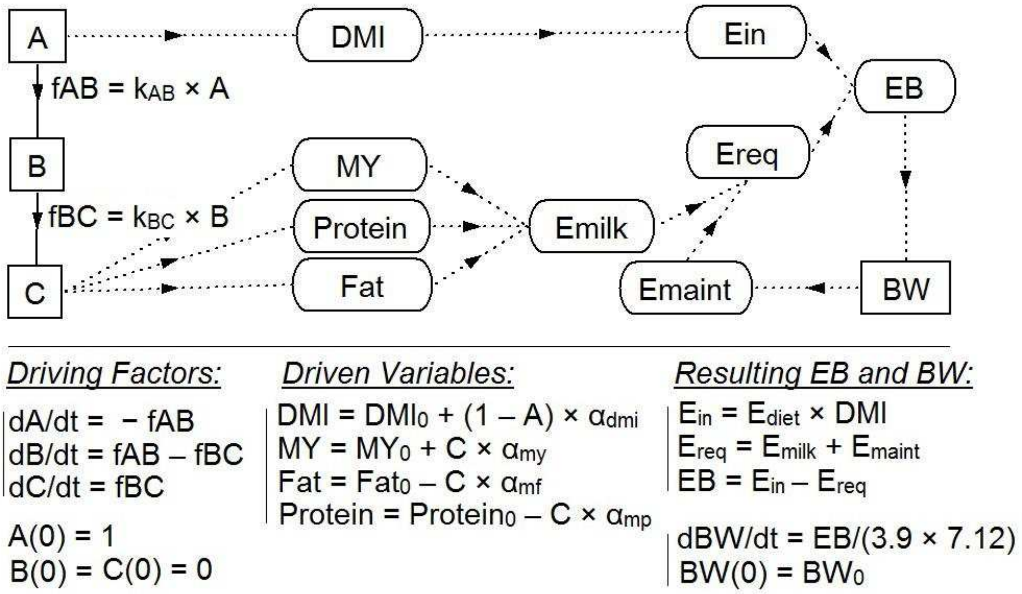

Figure 4. Diagram of the model showing the successive compartments of driving factors (A, B and C) used to model the regulation of the variables intake (DMI), milk yield (MY), milk fat and protein content during the onset of extended lactation in dairy goats. Fluxes are represented by continuous arrows and are named using "f" followed by the names of the 2 affected compartments. Forrester's symbolism is used: boxes = compartments; ovals = variables; solid arrows = flux of matter, dotted arrows = flux of information. Differential equations and parameter definitions are presented in the appendix and Table 1.

The simulated adjusted variables were then used for the calculation of energy balance (EB, Figure 4), assuming that energetic inputs (E_{in}) result from DMI multiplied with the estimated net energy content of the diet (E_{diet}). Energetic requirements (E_{req}) for milk production and maintenance were defined according to the equations of Sauvant et al. (2007) (Appendix). The resulting EB is equivalent to the net energy available for any change in BW, so this was used in the model to compute theoretical BW changes and thus the BW evolution during the onset of EL.

The number of parameters (11) estimated using the group average profile is relatively high regarding to the number of variables observed (5), thus not surprisingly, the fit was globally good as shown in Figure 3 (continuous lines) and quantified in Table 2 (two first columns). Globally, the model was able to describe an average time profile of performance (mean CD = 75% for the 5 variables observed), except for milk fat content and EB where the model simulated a consistent tendency but failed to track some of the systematic variation that were observed around the general trend (Figure 3B and C). The internal consistency of the model, as estimated by EB and the resulting BW, agreed with observations (Figure 3B), especially after 30 d. As there was a relative lack of data and higher variability during the first 30 d of simulation, model outputs during this period require cautious consideration. Given this, the model seemed to correctly represent an average energy partitioning at the onset of EL and validated the hypothesis of a global delay in the transfer of energy from feed to milk at the onset of EL. This global delay (sum of $1/k_{AB}$ and $1/k_{BC}$) was of 45 d (Table 1). About 85% of it was related to the rate of increase in DMI (due to the mean residence time of A of about 38 d) whereas the remaining 15% was related to the time-lag between the increase of DMI and MY (due to the mean residence time of B of about 7 d). After accounting for the maintenance requirements, the coefficient of partition between milk and body gains (P_{milk}) calculated from the model indicated that, on average there is a high proportion (75%) of energy going to milk during the first 90 d of EL. P_{milk} increased from 67% at wk 1 of EL to 81% at wk 13.

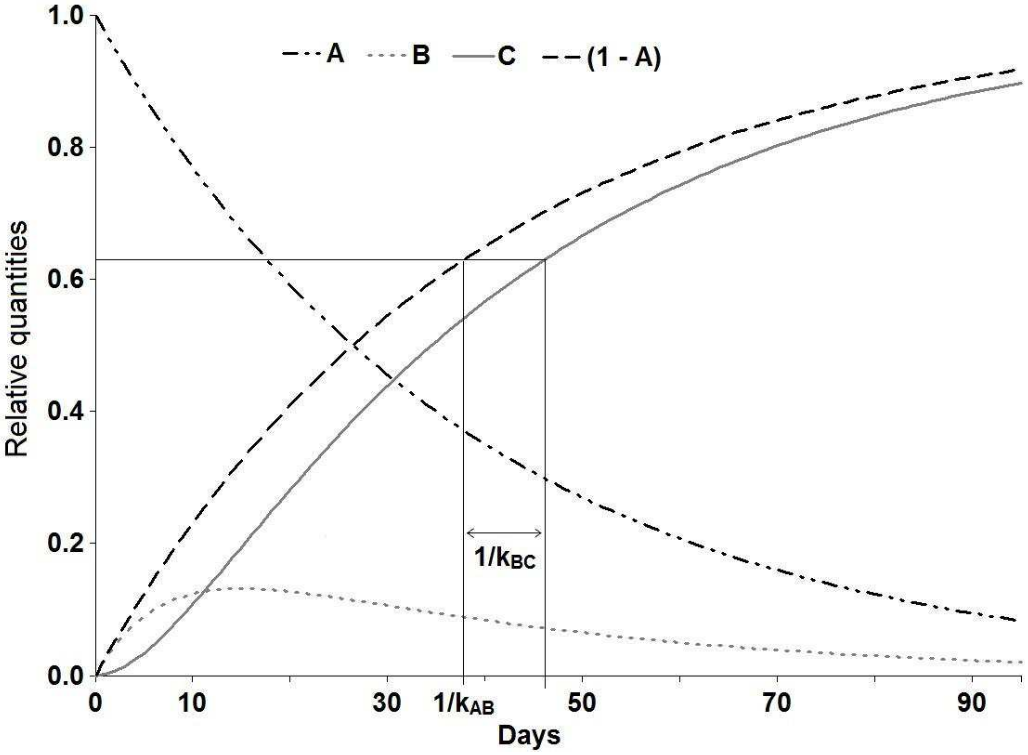

Figure 5. Relative quantities of the driving factors A, B and C resulting from successive first-order reactions A → B → C and used to represent the regulation of DMI (1–A) and MY (C) during the onset of extended lactation in dairy goats.

Model Ability to Fit the Range of Individual Profiles

Additional simulations were done to assess the ability of the model to fit a range of individual profiles at the onset of EL. For this, the observed performances of the 20 individuals during the onset of EL were used. Individual differences explained a high proportion of the total variability observed in the 5 variables: 70% for DMI, 58% for MY, 63% for Fat, 52% for Protein, 74% for EB and 94% for BW (data not reported). Thus the data set of individual observations seemed to be a good candidate to assess the model ability to fit a range of profiles at the onset of EL. The initial parameters (DMI_0, MY_0, Fat_0, $Protein_0$, and BW_0) were thus adjusted individually to simulate the individual profiles. The values of the 7 others parameters were kept from the calibration to the group average profile, assuming that the dynamic process was the same for all individuals after determining the vector of initial values (Table 1). The results are shown in Table 2 and Figure 6. Once the initial values of the estimated group average profile have been adjusted individually, a large improvement of the fit was obtained with BW observations, as the resulting RMSE was close (+22%) to that obtained with the group average profile. For the other variables, much more time-variation was observed and consequently the error improvements were not so good. In particular, it seems that the time-variations from the different variables were aggregated in the calculated values of EB, which can explain the high RMSE for this variable. The low CD_{RES} (- 8.2%) reported in Table 2 is illustrated in Figure 6. The model seemed to correctly explain the average differences in EB between individuals (white squares) but much less so the within-individual variations (grey points) around every average value. Nevertheless, the model described on average 44% (mean of the 5 first CD_{RES} of the last column of Table 2) of the intra-individual variability observed in the 20 time-profiles. Thus, merely adjusting the initial values and not the scaling parameters seemed to allow a substantial integration of individual variations. No systematic bias was obvious for the 6 variables (Figure 6)

Table 2. The Root Mean Square Error (RMSE) and the coefficient of determination (CD) of the model when fitted to the average profile data, and to the individual profiles data (n=20)

Data Set of Observations	***Average Profile***		***Individual Profiles (n=20)***	
Parameters Adjusted[1]	***All***		***Initial Values***	
Variables	***RMSE***	***CD***	RMSE	***CD_{RES}***[2]
DMI (kg/d)	0.065	84.4%	0.196	20.7%
MY (kg/d)	0.078	95.6%	0.237	67.1%
Fat (%)	0.150	37.0%	0.342	10.9%
Protein (%)	0.082	76.0%	0.141	48.6%
BW (kg)	1.064	75.7%	1.217	70.2%
EB (MJ/d)	0.575	15.6%	1.345	- 8.2%

[1] "All": all the parameters used in the model are those derived from the group average profile. "Initial Values": only the initial parameters (DMI_0, MY_0, Fat_0, $Protein_0$, and BW_0) were adjusted individually, the values of the other parameters are those of the group average profile (Table 1)

[2] CD_{RES}: Coefficient of determination calculated with the residual sum of square of the observed data for each variable (see Material and Methods)

To explore further the individual relationships between performances during EL, a PCA was performed on the initial parameters estimated (DMI_0, MY_0, Fat_0, $Protein_0$, and BW_0) and the average EB (EB_{90}) and ADG (ADG_{90}) calculated over the first 90 d of EL (Figure 7). The two first axes of the principal components (PC) accounted for respectively 40.2% and 30.2% of the total variation (Figure 7A). PC1 discriminated low from high values of EB_{90} (r = 0.97) and ADG_{90} (r = 0.97), whereas PC2 indicated that, independently from PC1, high levels of MY_0 (r = 0.85) and BW_0 (r = 0.53) were associated with low milk protein (r = − 0.70) and fat (r = − 0.43) contents at

T_{change}. DMI_0 was positively correlated (r = 0.64) as much with PC1 as with PC2. The interpretation of these results was helped by the projection onto the plot of non weighted supplementary variables reflecting the average performances measured over 300 DIM in period n−1 (MY_{n-1}, BW_{n-1} and BCS_{n-1}), as well the age and litter weight at last kidding ($LitterWeight_{n-1}$). The BCS (BCS_{90}) and milk efficiency (EFF_{90}) observed on average over the first 90 d of EL were also used as these variables were not simulated in the model. These two last variables were opposed on PC1, so observations concurred with model predictions on the interpretation of PC1 as being an axis that distinguished the partition of energy intake towards body reserves (right side) or milk (left side) during the onset of EL. Subsequently, the variations in BCS_{n-1} and BW_{n-1} were found to be highly correlated with those estimated at T_{change}, whereas MY seemed less correlated across time.

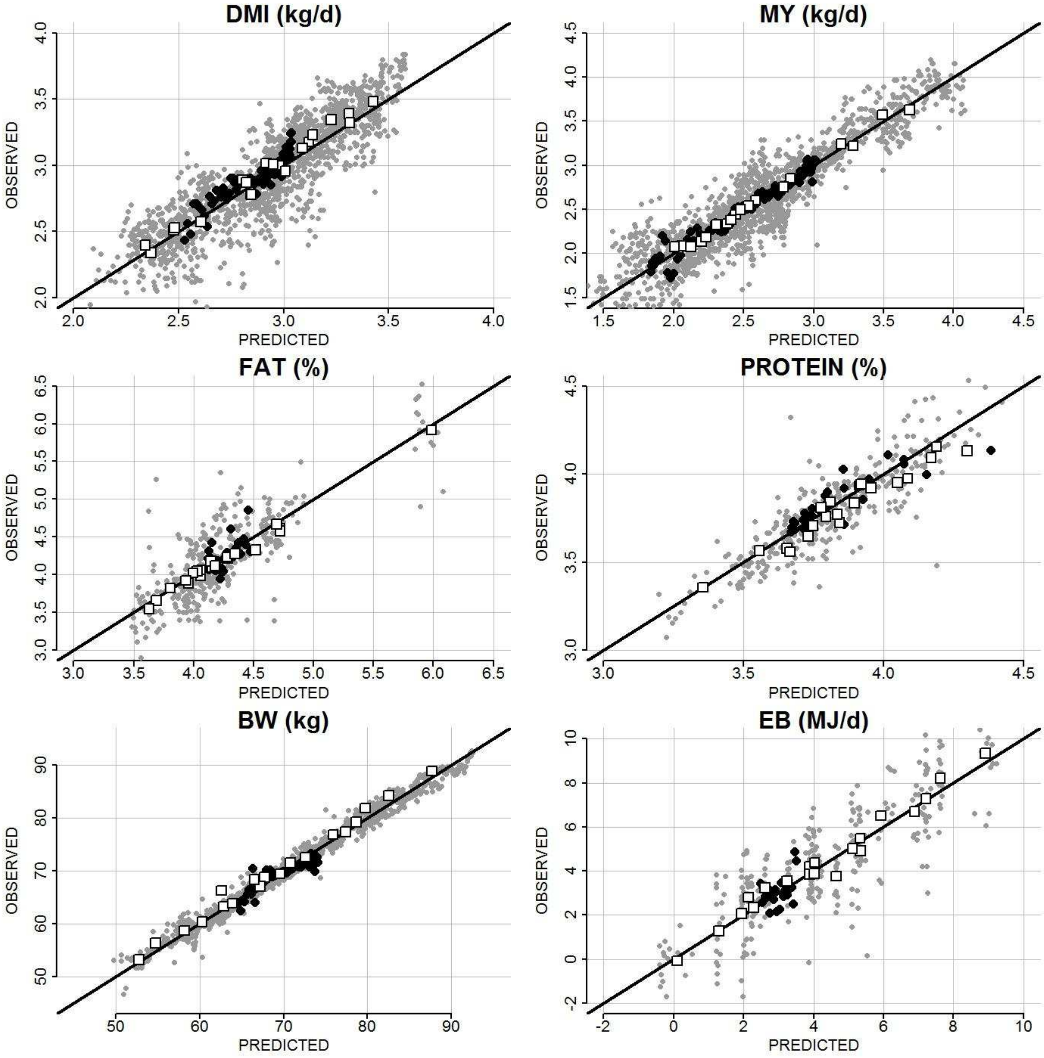

Figure 6. Observed and predicted values of the state variables milk yield (MY), dry matter intake (DMI), Fat and Protein contents in milk and body weight (BW) for the group average profile (black) and the 20 individual profiles (grey) at the onset of extended lactation. The average values of the 20 individual profiles are also shown (□).

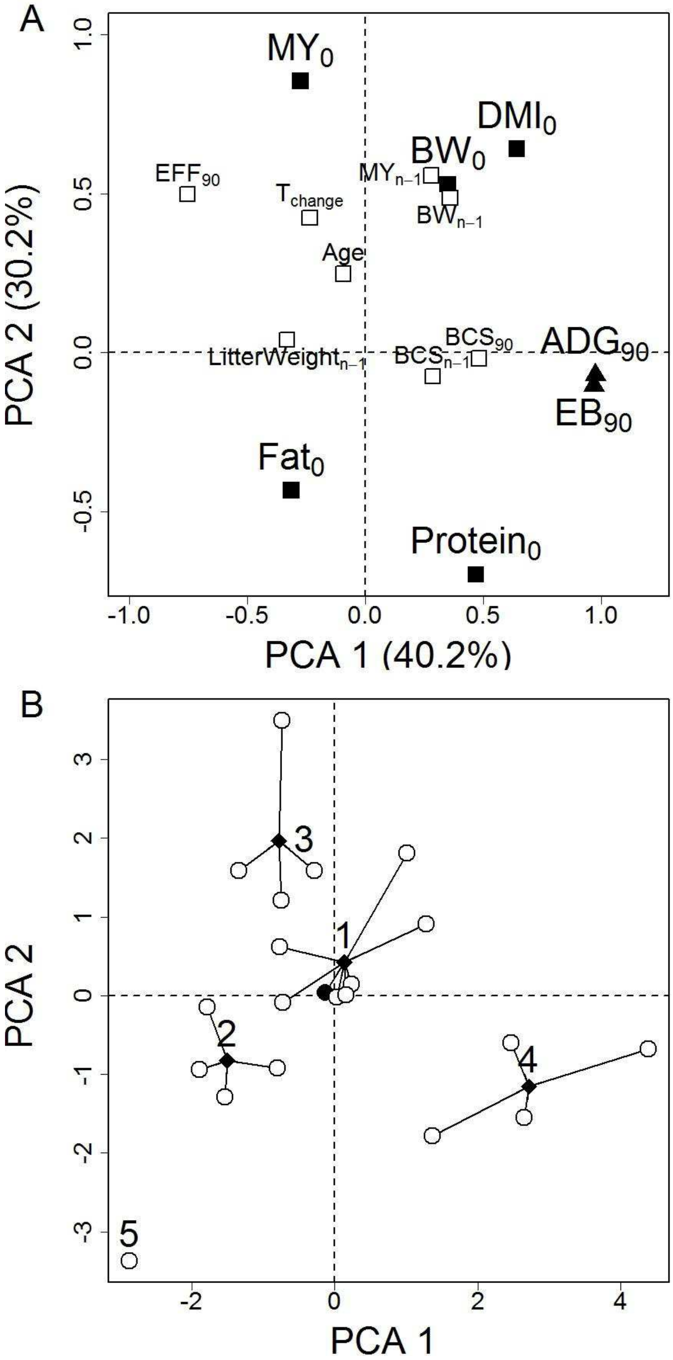

Figure 7. A) Plot of the first 2 principal components of a PCA performed on the estimated values (■) of initial parameters (DMI$_0$, MY$_0$, Fat$_0$, Protein$_0$, and BW$_0$; See Table 1 for definition) and on the predicted values (▲) of average energy balance (EB$_{90}$) and daily gain (ADG$_{90}$) over the first 90 d of EL for the 20 individual profiles. Non weighted supplementary variables (□) were added to the plot to aid interpretation. Subscripts “n−1” and “90” indicate respectively an average daily value over the first 300 DIM and the first 90 d of EL. See text for explanation. B) Score plot of the 20 individuals (○) and the non weighted average profile (●).The 5 different clusters obtained after HCPC were used to project their respective barycentre (♦), as identified with their number from 1 to 5.

The score plot (Figure 7B) shows the 20 individuals clustered in 4 main groups according to their score on PC1 and PC2. During period n-1, Group 1 (n=7, including the average profile) and Group 2 (n=4) were respectively the groups with the highest and lowest values of BW, BCS and MY. Thus, these 2 groups seemed to distinguish high (top right) from low (bottom left) potential for NL. Over the first 90 d of EL, Group 3 (n = 4) had the highest average MY (3.38 ± 0.111 kg/d) compared to the 3 others groups (all below 2.5 kg/d), In contrast, during the same period, Group 4 (n = 4) showed the lowest values for both efficiency and MY. Thus, these observations seemed to indicate a preferential energy partition toward milk (top left) or toward body tissue gain (bottom right) at the onset of EL. This was confirmed with the average partition coefficients (P_{milk}) calculated with the model over the onset of EL as Group 3 had the highest value (81.5%) whereas Group 4 had the lowest (58.2%). Moreover, individuals with the lowest performances during NL (Group 2) tended to partition their energy similarly to Group 3 during EL (P_{milk} = 80.3%). This partition to milk was even greater than individuals with the highest performances during NL (Group 1; P_{milk} = 72.3%).

DISCUSSION

This study characterized the time-profiles of performance of dairy goats undergoing extended lactation by comparing their milk production and BW with those of goats having two successive normal lactations and by modeling the changes in milk production, BW and DMI at the onset of EL. To our knowledge, this is a first attempt in dairy goats to describe the relations between concurrent energy functions during EL, because previous investigations have mainly focused on the lactation curve or on milk production (Salama et al., 2005; Chastin et al., 2001; Linzell, 1973a). Beyond showing that EL goats could produce as much milk as NL over 2yrs, this study demonstrates that EL efficiency depends both on an increase in resource acquisition and on the potential of goats to partition energy from the diet towards milk production instead of to body tissue gain.

Comparing the evolution of MY, fat and protein content and SCC during EL with those of two successive NL suggests that in terms of milk production, EL is more analogous with a new lactation, i.e. an increase to “peak phase” followed by a “persistency phase” (Gipson and Grossman, 1989), rather than with a simple extension of NL. EL goats showed higher persistency than NL-pregnant goats due to the negative effect of pregnancy on MY, which was detected from wk 7 after conception. This was close to the results reported by Knight and Wilde (1987; 8wks) and Salama et al. (2005; 10 wks). Although the persistency phase was about one month longer for EL goats than NL, the onset of EL was primarily characterized by the initiation of a second peak phase lower but longer than the normal peak phase (Figure 1A). During this phase, a dilution effect can lead to higher milk fat and protein content in milk of EL compared with NL (Salama et al., 2005). However our study does not support this for milk fat as there was no significant difference between EL and NL (Figure 2).

In terms of BW, it is clear from the observed profiles that EL goats differ substantially from NL. The most striking difference was the rapid and very high BW increase (+ 9.3 kg with an ADG of 60.4 g/d) that was observed concurrently with the increase of MY (Figure 1B). These BW gains appear exceptionally high compared with references to goats regaining body reserves during a NL (between wk 7 and 27) being twice that of goats in parity 2 and four times that of goats in parity three or more (Sauvant et al., 2012). BW variations could also be due to variations in gut fill, notably because EL goats were increasing their DMI when the rise in BW was observed (Figure 3). However the calculated values of EB were largely positive during the onset of EL (+ 3.03 ± 0.13 MJ/d for the average profile) and tended to progressively decrease consistently with the asymptotic trend in BW. Thus, this seems to indicate that the observed increase in BW of EL goats was mainly due to body reserve accumulation. Conversely, EL goats showed almost no increase in BW as MY declined, neither from wk 37 to T_{change} in period n – 1, nor from wk 23 to wk 39 (wk 6 of pregnancy) in period n. Furthermore, EL goats reach a BW similar to NL goats by the end of pregnancy in period n. Collectively, BW and MY profiles suggest that a key effect of EL on dairy goat performance is to disrupt the phase opposition between MY and BW dynamics which usually takes place during NL.

The results from modeling the onset of EL do not support the proposition that the rise in MY drives the increase in resource acquisition, as it is generally assumed at the onset of a NL. In contrast, it suggests that DMI is the driving force responsible for the increase in both MY and BW. In this experiment, the feeding conditions were constant: the quantities of dry matter offered were non-limiting and the diet was of high energetic value, thus it can be considered that the increase in DMI did not result from a feeding effect. Another possible reason for observing an increase in DMI during the reproductive cycle can be increasing requirements for covering particular physiological functions (e.g. lactation, gestation). The present observations do not support this hypothesis because MY appeared to be delayed compared with DMI and EB remained positive during all the period. In the model, a time-lag of about 7 days (equal to $1/k_{AB}$) was found between the increase of DMI and the increase in MY. Consequently, in this study DMI seems to be the driving force of the changes at the onset of EL.

However a critical assumption reflected in the model structure was that the BW dynamic is a consequence of DMI and milk production rather than a possible driving force at the onset of EL. The main reason for that assumption was to allow the use of body energy changes as a means to check the internal consistency between the parameters related to the dynamics of the different measured items. It is well known that body energy change can be an important driver during certain periods of the reproductive cycle when females regain body reserves (Friggens et al., 2004). However, our comparative approach (Figure 2) suggests that before T_{change} the most important gains in BW are related to the pregnancy of a NL whereas BW of EL goats increased noticeably only after T_{change}. This is consistent with previous studies in dairy cows that showed a pregnancy effect on body reserves storage (Friggens et al., 2010). In our experiment, the relative lack of data on BW and DMI for the first 2 wks at the onset of EL prevents any clear opinion about the driving force at the onset of EL in goats. Whilst it is not possible to exclude the possibility of BW being a significant driver, the observed data from the end of period n-1 together with the coherent simulation results from period n do not provide any contradiction with the suggestion of DMI being the driving force.

The model presented here operates at a high level of description, thus it does not attempt to describe the mechanisms that activate the increase in DMI but merely opens questions on its origin. Season has been put forward as a possible trigger for resource acquisition and the effect of photoperiod on MY and DMI has been explored in seasonal breeders like sheep (Bocquier et al., 1997) and goats (Garcia-Hernandez et al., 2007). It is generally reported that an increasing photoperiod stimulates first MY and then DMI during a NL whereas our study showed that DMI increased first at the onset of EL. Furthermore, our study agrees with other studies on EL where T_{change} occurred in decreasing daylight, at the beginning of the winter in Spain (Salama et al., 2005) or in France (Chastin et al., 2001). Thus, it can be assumed that the activation of T_{change} is not related to the photoperiodic effect reported during NL. In Chastin et al. (2001), T_{change} occurred at the same month for goats that kidded either in December or in February in period n-1, thus T_{change} might be primarily triggered by clues as to the time of the year. However, Linzell (1973) observed that MY of EL goats varied cyclically even with a constant long day photoperiod but their cycle was shortened by about 5 wks compared with natural light changes. Therefore, T_{change} might reflect an innate seasonal adaptation of goats which is nevertheless subject to some effect from the rate of change in daylight.

Different physiological mechanisms under seasonal control exist and can underlie the changes of relations between DMI, MY and BW (Lincoln et al., 2003; Rhind et al., 2002). If DMI increases first during an anabolic growth-phase (and not as a consequence of a greater energy requirement from the mammary gland), this can be the result of a neural mechanism which controls a long-term cycle in food intake and body weight (Lincoln et al., 2001). Even for farm animals, such cycles can persist under constant conditions of temperature and light, as was the case for the seasonal cycles in MY observed by Linzell (1973) during EL. In the present study, these long-term cycles in MY during EL seem to be driven by cycles in intake. However, the onset of EL (T_{change}) occurred during the short-days, at the beginning of winter, whereas the usually reported pattern of the cycle in non-reproductive animals is an increase in intake and BW during long-days, from spring to autumn, when food is usually abundant under natural conditions. The evidence from the present study suggests an additional seasonally cued driver linked to the reproductive cycle. Linzell (1973) observed seasonal variations in udder volume along with those of MY during EL, even when goats were ovariectomized. This suggested anticipatory mammary growth, occurring independently from the gonadotrophin axis. Although there is no clear evidence to identify the endocrine mechanisms involved, it can be speculated that the disruption of the phase opposition between MY and BW dynamics observed during EL is the consequence of an anticipatory anabolism, interacting with the lactotroph axis. Clearly, this issue warrants further investigation with the appropriated measures at a physiological level.

Adjusting only the initial parameters values of the model allowed a substantial incorporation of individual differences. This suggests that the performances over the first 90 d of EL are largely predetermined by the animal state at T_{change} (as described with DMI_0, MY_0, Fat_0, $Protein_0$, and BW_0). Potentially there are at least two interesting implications from this. First, a predetermined trajectory can allow better prediction of goat performance at the onset of EL and thus allow the appropriate feeding strategy to be used. Second, this suggests that the potential of goats for EL can be estimated from T_{change} and used to develop new criteria for the improvement of culling strategies. This relies on the assumption that the first 90 days of EL are representative of a potential for EL. Fully exploring this assumption is beyond the scope of the present study and would require much more data than was available in the present study. However, under this assumption our analysis suggests that there is no clear relation between the potential for NL (as estimated by MY_{n-1}) and the potential for EL. In our analysis, it is suggested that the potential for EL is positively associated with lactation persistency (in period n-1) as the more productive goats during the onset of EL (e.g. Group 3) had both a high DMI and MY at T_{change}. Goats with a high milk production in $period_{n-1}$ that did not fulfill these conditions (e.g. Group 1) tended to partition a considerable amount of energy towards body reserves instead of milk. However when considering efficiency rather than MY during the onset of EL, there can be some goats (e.g. Group 2) that are good performers during EL despite a relatively low production and persistency during period$_{n-1}$. From this view, the potential for EL could depend more on the goats capacity to partition energy from the diet towards milk production instead of to body tissue gain rather than on absolute levels of DMI and MY.

Although in the present study we could only model the onset of EL, i.e. the first 90 d, it would be of interest to extend this approach to provide information about peak yield and persistency of EL. This is an issue that is usually explored with lactation curves models (Steri et al., 2012; Dematawewa et al., 2007; Gipson and Grossman, 1989). However, even if models of NL curves have been fitted successfully to monotonically decreasing EL in dairy cows, they will probably not be flexible enough to accommodate the characteristic fluctuations depicted in the EL profile in dairy goats and a specific function may need to be developed. With the present model, no attempt was made to represent the transition between the persistency phase of NL and the onset of EL. Even if the compartmental structure provides an elegant way to describe the regulation of performances at the onset of EL with a limited number of state variable, it cannot accommodate the disruption of the phase opposition between MY and BW dynamics, which has been suggested by the comparative approach. Complete nutritional models based on the same principle of a compartmental regulating structure are able to represent complex dynamics during NL (Puillet et al., 2008; Martin and Sauvant, 2010), thus they can be adequate candidates for incorporating the predetermined trajectory of EL which has been suggested here.

CONCLUSION

The unified characterization of milk production and BW evolution for dairy goats undergoing EL provided evidence that a key effect of EL is to disrupt the phase opposition between MY and BW dynamics which usually takes place during NL. This effect appears to be primarily driven at the onset of EL by a predetermined increase in resource acquisition, and is then characterized by a delayed transfer of energy from feed to milk. The individual variability observed in the relationships between milk production, live weight and intake at the onset of EL suggested that suitability of goats for EL is mostly based on a tendency for partitioning energy towards milk production instead of to body tissue gain during the onset of EL and possibly on a high NL persistency.

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APPENDIX: Model Equations

Differential equations are presented below and parameters values and definition are given in Table 1. The INRA system is used to calculate energy balance, so for all physiological functions, the same efficiency is assumed to convert metabolizable energy to net energy.

Compartments of dimensionless matter: A, B and C

$dA/dt = -fAB$

$dB/dt = fAB - fBC$

$dC/dt = fBC$

$fAB = k_{AB} \times A$

$fBC = k_{BC} \times B$

$A(0) = 1$

$B(0) = 0$

$C(0) = 0$

Variables driven by A, B and C

$DMI = DMI_0 + (1 - A) \times \alpha_{dmi}$

$MY = MY_0 + C \times \alpha_{my}$

$Fat = Fat_0 - C \times \alpha_{mf}$

$Protein = Protein_0 - C \times \alpha_{mp}$

Variables of the energy balance calculation (MJ/d)

$E_{milk} = (MY \times (0.4 + 0.055 \times (Fat - 3.5) + 0.033 \times (Protein - 3.1))) \times 7.12$

$E_{maint} = (0.79 + 0.01 \times (BW - 60)) \times 7.12$

$E_{req} = E_{milk} + E_{maint}$

$E_{in} = E_{diet} \times DMI$

$EB = E_{in} - E_{req}$

$P_{milk} = E_{milk} / (E_{in} - E_{maint})$

Body weight estimation from EB

$dBW/dt = EB/(3.9 \times 7.12)$

$BW(0) = BW_0$

Paper 3

Synergy between selection for production and longevity and the use of extended lactation: insights from a resource allocation model in a dairy goat herd

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In preparation for the *Journal of Animal Science*

Introduction

Selection where the primary focus is for increased milk yield has historically worked well in a favourable environment (Kelm and Freeman, 2000). However, when faced with nutritional constraints, genotypes selected for high production in a favourable environment have survival and reproduction rates that are decreased with respect to genotypes which have been selected on these latter criteria during several generations (Pryce et al., 1999; Dillon et al., 2006; Savietto et al., 2013). In dairy livestock, this development of environmental sensitivity increases the risk associated with a narrow, milk production focused breeding strategy when it is practiced intensively for several decades, especially if future environmental conditions become more variable. For managers, it is economically desirable to achieve high levels of efficient production (Veerkamp, 1998). However, it is also economically important to minimize the risk of impairing functional traits, such as survival and reproduction, as they sustain the herd production process over the long term. At the herd level, two kinds of options may exist to compensate for environmental sensitivity; management and selection. A first option is to adjust herd management to better match the resource inputs to the animal requirements, either by manipulating the plane of nutrition, e.g. segmentation of the feeding plan instead of flat feeding, or by manipulating the level of resource requirements, e.g. widen the reproductive period to spread the herd resource requirement throughout the year (Puillet et al., 2010). Another option is to adjust the local selection objectives, i.e. the criteria considered to select the parents of future generations of productive animals (Calus et al., 2005).

Both options may be appropriate, and to some extent they interact. Tactical adjustments of herd management take place in a herd context but affect the within-life nutritional responses to the herd environment of individual animals. This individual response impact on the performance (including reproduction and survival) of individuals and thus shapes the selection responses observed in the long-term. It seems therefore essential to better understand this interaction to explore which management decisions would allow a satisfying system design to be found both in terms of short-term efficiency and functional longevity.

Extended lactation (**EL**) is sometimes practiced to avoid the culling of high producing dairy females that failed to reproduce (Butler et al., 2010), especially in goats (Salama et al., 2005; Douhard et al., 2013). Although EL seems an interesting option to compensate or anticipate the undesirable effects of environmental sensitivity, its benefit probably depends on the variability of resource availability in the herd environment. When a high quality nutritional resource is provided constantly in large quantities, EL may be counterproductive as it slows down the genetic progress within the herd. It also means less milk production on average per milking goat which is economically disadvantageous. Conversely, when there is variability in resource availability it can be a temporal buffering strategy. However, when resource availability varies considerably, EL may not be sufficient to compensate for the negative effects of environmental sensitivity in high producing genotypes. In this case, it may be more advantageous to select for robust genotypes that are able to accommodate a large range of environmental limitation, even if this reduces the genetic progress achieved in milk yield. In practical terms, selection for robustness can be achieved by giving a positive value to age –in addition to milk yield– in the local selection process. The objectives of this study were to quantify the influence of EL when selection for robustness was applied in a herd facing different levels of environmental variability across time.

MATERIAL AND METHODS

Model Overview

Figure 1 presents the main processes that make up the herd simulation model used in this study and described in details in Douhard et al, (in prep). The model was individual-based, discrete-time and combined a weekly cycle (left handside), which represents the nutrition process, with a yearly cycle (right handside), which represents selection and mating processes.
The key point linking the two cycles was that every individual in the herd was characterized by heritable traits of resource allocation affecting its weekly performance. Several traits of this observed performance were recorded during year n−1 on used as criteria to select individuals that will be parents in the next year n. Moreover, during the mating process selected parents that reproduced successfully transmitted their heritable traits to their offspring. Once a year, surviving individuals were evaluated based on both i) criteria of observed phenotypic traits of performance and ii) the selection weights defined in the manager's selective breeding strategy and which reflect the importance given by the manager to the different traits. These informations were combined in a selection index (**SelIndex**) used to rank the candidates and select them. Based on their SelIndex score, a fix proportion of the best candidates were selected to be parents in year n, whereas the remaining proportion was voluntarily culled and replaced with the offspring born during the year. In our case, young individuals chosen for replacements came from the herd and were sons and daughter of the elite adult females (those that had the greatest SelIndex, i.e. pedigree selection).

Overall, parent's selection and their replacement (reflecting part of the manager's priorities) along with inherent variation in individual survival and fertility (reflecting part of the animal's priorities) bring about genetic progress in the herd.

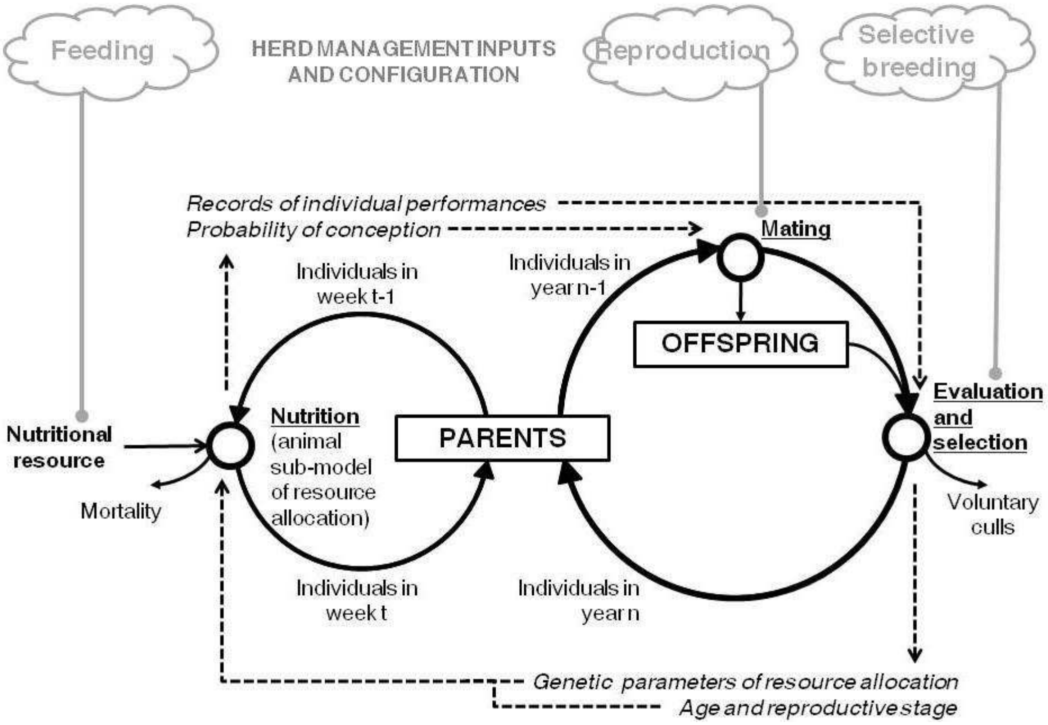

Figure 1: Overview of the 3 main processes that make up the herd simulation model. The nutritional responses of individuals chosen to be parents are represented on a weekly basis (small cycle). It determines their individual survival (i.e. the risk of involuntary culling), their probability of conception during the mating process and their performance. These performances, in turn, are used during the evaluation/selection process. Mating and selection processes are represented on a yearly basis (large cycle). It determines reproductive success and distinguishes those individuals that are selected to become parents from those that are voluntary culled and replaced. These 2 processes, in turn, lead to differences of age and reproductive stage that affect the nutritional responses. The grey clouds and connectors indicate where herd management decisions affect the 2 interdependent cycles. Other symbols represent compartments of individuals (boxes), physical flows (solid black arrows), information flows (dotted arrows) and processes (circles).

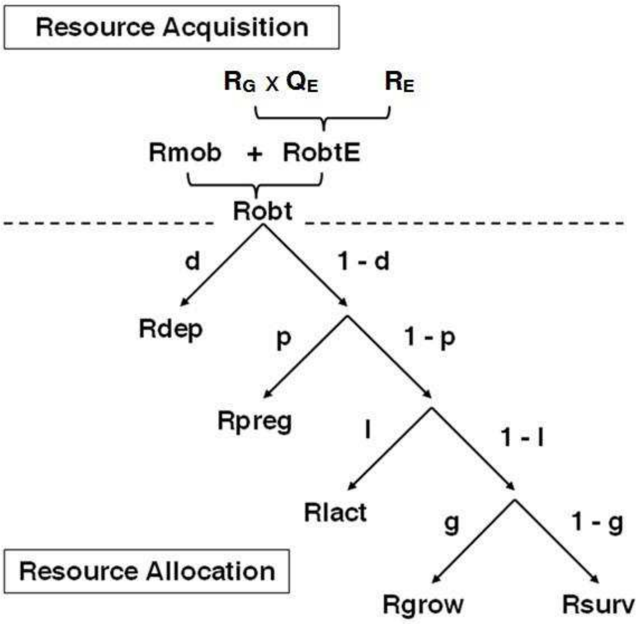

Figure 2: Schematic representation of the resource acquisition process and the hierarchy of resource allocation between functions. The animal has a potential for resource acquisition (R_G) which is achieved or not depending on the resource quality (Q_E) and the resource availability in the environment (R_E). The sum of resources obtained (Robt) from the environment ($Robt_E$) and from the body reserves (Rmob), is then allocated between body reserves deposition (Rdep), pregnancy (Rpreg), lactation (Rlact), growth (Rgrow) and survival (Rsurv). At each level of the hierarchy, coefficients d, p, l and g describe the proportion of the available resource which is allocated, and the remaining proportion available for the next level down. In the case of nutritional constraint (i.e. a decline in Robt), some allocation plasticity allows the coefficients to be decreased to give priority to survival. In this case, the proportion of Robt which is allocated to survival is increased ($s = (1 - d) \times (1 - p) \times (1 - l) \times (1 - g)$).

Desired resource acquisition. The animals ability to acquire resources is modeled as being a function of body size (BWnl) and level of body reserves (BR), according to principles described by (Tolkamp et al., 2006, 2007). Genetic variation in resource acquisition (R_G) comes about indirectly through the implicit relationships among the energy partitioned off for lactation and BR deposition, and the remaining energy available for growth (Fig. 3). In this way, animals that partition less energy into lactation and BR deposition will have more energy available for growth, leading to a larger BWnl throughout the life of the animal and therefore greater rates of R_G. Further, because R_G is also dependent on BCS (i.e. the level of BR relative to BWnl), genetic variation in R_G also comes about indirectly through genetic variation in parameter d. With low levels of d, the animal has lower body energy reserves, and as a consequence R_G will be greater.

Inclusion of EL aspect in the sub-model and calibration on a dairy goat profile

The model used for this study wand described in Douhard et al. (in prep) required some modifications to accommodate EL. The two main new features included were: 1) a transient increase in resource acquisition assumed to be triggered by a seasonal cue at about 330 DIM, and 2) an increase in resource allocation towards body reserves deposition (d) and towards lactation (l) occurring almost simultaneously with the change in acquisition. These were parameterized using the extended lactation data of Douhard et al. (2013) .

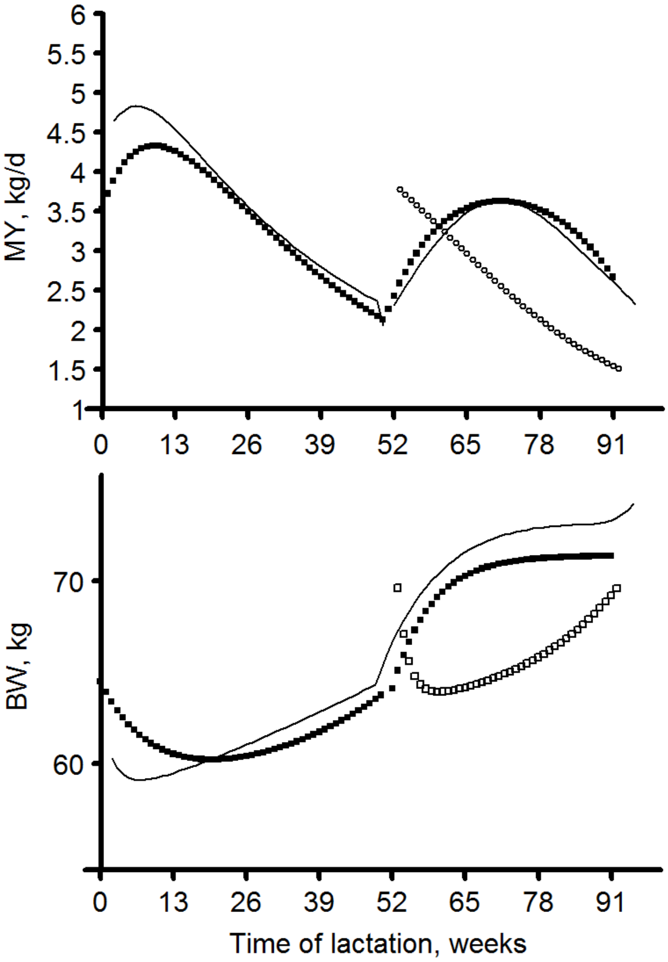

Figure 3: Time-profiles of milk yield (MY) and body weight (BW) for dairy goats undergoing extended lactation (black square). One year after kidding (at week 0), MY and BW increased. At this moment, MY and BW of goats that had a new parturition are indicated (white square). Data were smoothed values obtained from Douhard et al. (2013). Continuous lines indicate the fitted values of the model (obtained with l_0 = 0.8 and d_0 = 0.22).

Environmental Limitation and Variability

Environmental limitation was described as a level of resource availability, assuming a constant quality (Q_E). It was defined relative to the desired energy intake R_G (MJ/d) of each animal. Within age classes (less than, or greater than 1 year of age), the degree of environmental limitation was the proportion $\mathbf{P_{LIM}}$ of animals within the herd class for which feed availability was insufficient to meet levels of *ad libitum* intake. The amount of resource available for each individual ($\mathbf{R_E}$) was defined as the P_{LIM}th percentile in the distribution of the desired intake of the considered group. For each individual, $Robt_E$ was thus determined as follows:

$$Robt_E = \min(R_E, R_G \times Q_E)$$

In this study, 2 environments were simulated: a constant environment (K) which had an unlimited resource availability (i.e. $R_{obtE} = R_G \times Q_E$), and an environment with a variable availability (V). The different selection strategies were simulated according to 2 scenarios, shown in Figure 4. In the V-V scenario, animals and selection were simulated in the V environment for 40 years whereas in the K-V scenario, simulation occurred under a favourable constant environment for 20 years (K environment) followed by a further 20 years in the V environment. The level of environmental variability was defined both between years and within year. For each year, the annual average level of environmental limitation was sampled from a uniform distribution between a minimum P_{LIM} value and 1. For each week within a year n, the level of environmental limitation was sampled from a normal distribution with a mean equal to the simulated annual average level and with a standard deviation.

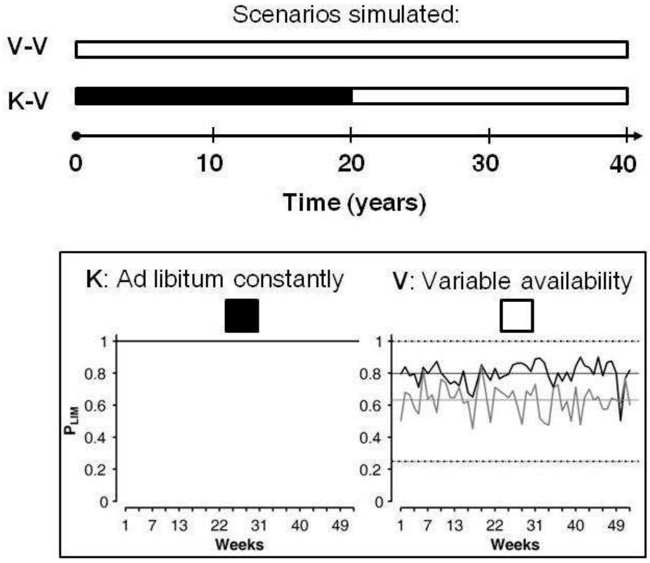

Figure 4: Definition of resource availability for 2 environments used in the scenarios simulated; the herd selection and production process occurs either in a variable environment during 40 years (V-V) or in a constant environment during 20 years before being transferred in variable conditions (K-V). In the box, one year of each environment is shown. In a constant environment (K), the proportion of animals fed ad libitum (P_{LIM}) is maximal across time, i.e. $P_{LIM} = 1$. In a variable environment (V), for each year there is an average proportion of the herd which is limited by resource the resource availability (e.g. 2 annual proportions are shown with continuous horizontal lines in the right panel). Each annual proportion is sampled from a uniform distribution between a minimum P_{LIM} value (P_{LIM0}, 0.25 in this study) and 1 (dotted lines). Within year, fluctuations in resource availability are defined weekly with a mean equal to the simulated annual average level and with a standard deviation (SD_{PLIM}, 0.15 in this study) (fluctuating continuous lines).

Selection strategies

In this study, 3 criteria were considered in the selection index (**SelIndex**) that defines the selection strategies implemented by the farm manager:

$$\mathbf{SelIndex = W_{MILK} \times MILK + W_{AGE} \times AGE + W_{PREG} \times PREG,}$$

where $\mathbf{W_{MILK}}$, $\mathbf{W_{AGE}}$ and $\mathbf{W_{PREG}}$ are the selection weights given by the manager to the different criteria **MILK**, **AGE**, **PREG**. MILK was the maximum energy corrected milk yield observed during the year, AGE was the age at the time of selection and PREG was the pregnancy status following the most recent mating period. The continuous variables MILK and AGE were standardized to avoid scale effects in SelIndex. The boolean variable PREG took the value 1 if the female was pregnant and -1 else to penalize females that failed to reproduce. Longevity (AGE) was interpreted as a robustness criterion in case of environmental limitation as the oldest females were expected to be those that successfully passed through the selection gate imposed yearly by the farmer and by the continuous natural selection.

Five different selection strategies were defined with different selection weights on age (W_{AGE} = 0, 0.05, 0.10, 0.25, 0.5) to study the effect of an increasing emphasis on longevity for the 2 scenarios simulated (V-V and K-V). In all cases, the weights on MILK and PREG remained the same, and both equal to 1.

In addition to the criteria included in SelIndex, the annual average body weight (**BW**) and body condition score (**BCS**) of each individual was described. Moreover, three measures at the herd level were calculated at the herd level; the survival rate (**SURV**) of year n was defined as the proportion of individuals that survived from year n to year n + 1, the reproduction rate (**REPRO**) was defined as the proportion of these living individuals that reproduced successfully during year n. The EL proportion described the proportion of females kept in year n + 1 despite a reproductive failure in year n.

Model initialization and parameterization

The model started out with a newborn base population, and initialization was undertaken for a period of 20 years in a K environment with a fixed replacement rate to keep a constant herd size. For this initialization period, voluntary culls were chosen randomly allowing equilibrium in both herd demography, as well as in average performances to be established.

The different strategies were simulated for 40 years with 20 herds replicated in each one. Performance based voluntary culling was set at a constant rate of 25% during selection. The number of replacement was determined to keep constant the total herd size (i.e. the number of individuals just after selection), here set at 500 females and 10 males. The 10 males were fully replaced every year.

RESULTS & DISCUSSION

Effects of different selection emphasis on age in a variable environment

Figure 5 shows the evolution of yearly responses to selection for milk yield when a different selection weight was simultaneously applied on age, in a variable environment (V-V scenario). As expected, increasing selection for age was consistently reflected in the survival rate (SURV): the greater W_{AGE}, the greater SURV simulated (except during the first 10 years for the 2 strongest selection strategies on age which initally caused a new demographic equilibrium to be set). Moreover, the 5 different selection weights on age led to different slopes of milk yield. These differences were expressed in the level of these patterns, as estimated by the mean of the last 5 years of selection (Table 1). Increasing the value of W_{AGE} led to a non-linear effect on the levels of MILK, and to a lesser extent of BCS and BW. For the 3 lowest selection weights on age (0, 0.05, 0.10), increasing W_{AGE} resulted in progressively decreasing MILK, and progressively increasing BCS and reproduction rate (REPRO). In contrast, herds selected using the 3 highest selection weights for age (0.10, 0.25, and 0.50) ranked the other way around. Milk yield improvement was even greater for a strong selection on age (Wage = 0.50) than for selection for MILK only, with SURV and REPRO levels being maintained at a relatively high level.

The change of direction in the response to selection for age was related to a net increase in the proportion of extended lactation (EL) in the herd (Table 1). This indicates that there is a value of W_{AGE}, between 0.10 and 0.25, above which the importance given to age in SelIndex is so high that older animals become systematically preferred regardless of their reproductive status. This had the effect of dramatically increasing the proportion of EL.

Lactating females that underwent EL had less cost energetic of gestation and lactation so this improved their probability to survive in the variable conditions. Contrarily to the peak lactation phase following parturition (Gipson and Grossman, 1989), females did not mobilize body reserves at the onset of EL when a new rise in milk yield is observed (Fig. 3, Douhard et al., 2013). Moreover they had more time to recover body reserves from their previous parturition. The consequence of these mechanisms within life allowed the allocation of resources to body reserves (and hence BCS level) to decrease across generations without a significant decrease in REPRO compared to the other strategies that selected for age. Apparently, the greater chance to reproduce successfully during EL could partly compensate for a high rate of reproductive failure during a "normal" lactation. Thereby older, high producing females could be preserved within the herd and drive a high milk yield progress.

This finding is congruent with observation in the modern dairy cow highly selected for production at the expense of a low fertility was better suited for EL than less selected strain (Kolver et al., 2007; Kay et al., 2009).

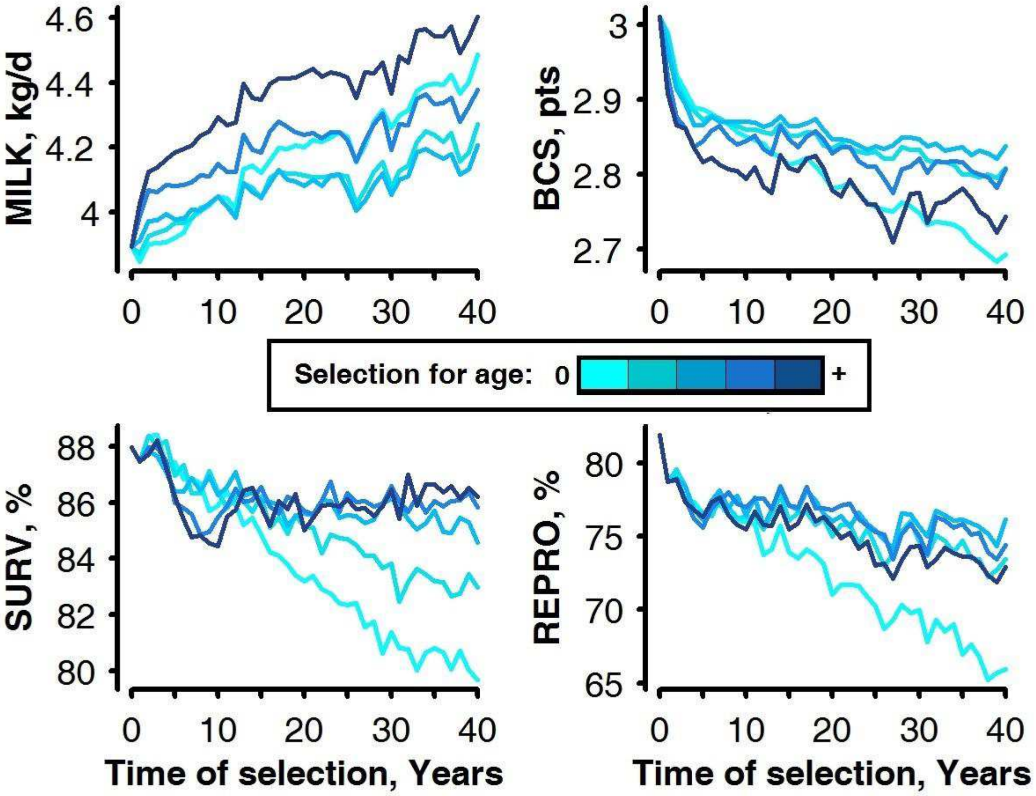

Figure 5: Responses in average individual performance to selection for milk yield combined with different weightings for age (0, 0.05, 0.1, 0.25, 0.5 with increasing density of shading) during 40 years in a herd provided with a variable resource availability (V-V scenarios). MILK: average peak milk yield. SURV and REPRO: survival and reproduction rates respectively.

Table 1: Performance means calculated over the last 5 years of simulated selection for milk yield and a different emphasis on age during 40 years in a herd provided with a variable resource availability (V-V scenarios). MILK: average peak milk yield. SURV and REPRO: survival and reproduction rate respectively. Each selection strategy was replicated 20 times.

	Selection weight on age (W_{AGE})				
Variable	0	0.05	0.10	0.25	0.50
MILK, kg/d	4.41	4.21	4.16	4.33	4.55
BCS, pts	2.70	2.80	2.83	2.80	2.75
BW, kg	60.7	59.8	60.0	62.4	65.3
SURV, %	80.2	83.0	85.0	86.0	86.4
REPRO, %	66.2	73.1	75.5	74.4	72.8
EL, %	0.7	1.1	3.3	10.5	19.4

When selecting for age, the non-linear response of MILK and BCS was explained at the level of the heritable traits of resource allocation. Figure 6 shows how these changes were associated with the proportion of EL. When the selection for age allowed only for a low proportions of EL (below about 5%), maintaining a high survival rate when selecting for milk yield was achieved by preserving a high resource allocation to body reserves deposition (d_0) and a moderate allocation to lactation (l_0). In contrast, as shown previously, greater proportions of EL relaxed the pressure to maintain high values of d_0. Contrarily to the strategies with the less emphasis on age, both allocations d_0 and l_0 decreased. Across generations, resource driven away from body reserves was thus mainly reallocated to growth and survival (Fig. 2) instead of to lactation. Therefore the higher MILK observed for the strongest selection for age (W_{AGE} = 0.25 and 0.5) was mainly caused by a greater desired intake R_G (due to the negative feedback of BCS on R_G and the greater body size). The study of Kolver et al. (2007) shows also that cows weel suited for EL had not only a high genetic potential for milk yield but were also larger and leaner than others.

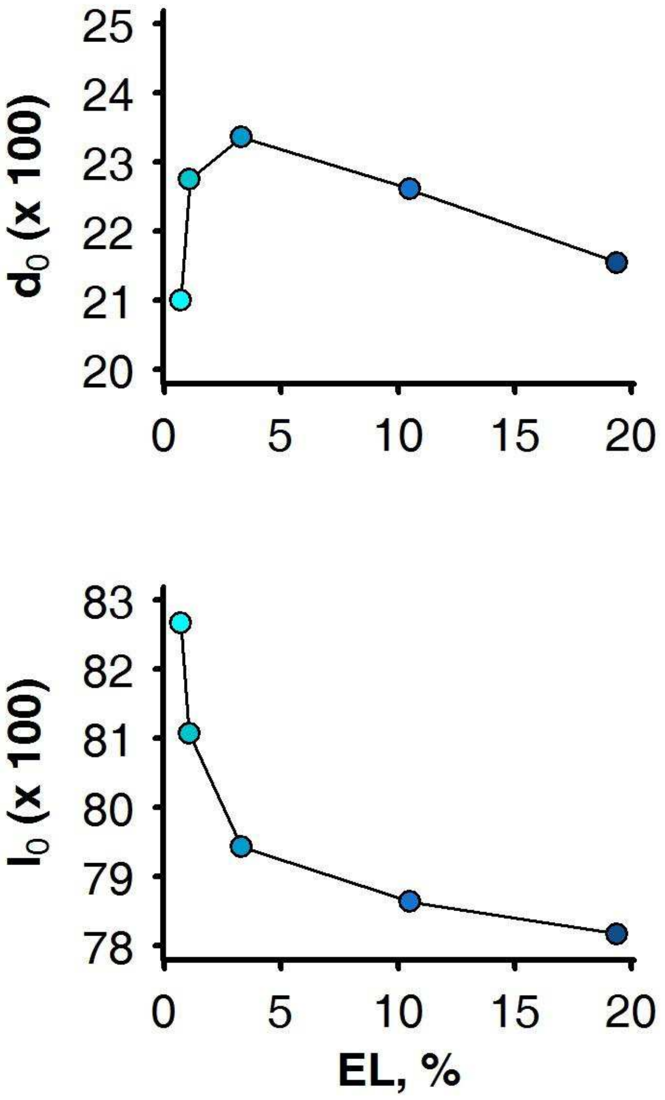

Figure 6: Relationship between the proportions of extended lactation in the herd (EL) and the average value of heritable traits of resource allocation for body reserves deposition (d_0) and for lactation (l_0) obtained after 40 years of selection for milk yield and a different emphasis on age (increasing density of shading of the points, as used in Fig. 5) in a variable environment (V-V scenario, see Material and Methods for scenario definition). Values are the means of the last five years of selection (20 replicates).

When MILK and SURV of the last five years of the different selection strategies in the V-environment (Fig. 5) were plotted together (Fig. 7), a trade-off was apparent (grey line) but was alleviated for the strongest selection for age. The top panel shows that as long as the proportion of EL remained low (circles), putting more emphasis on age improved survival but this was achieved by a trade-off with milk yield (grey lines) because the limited quantity of resource obtained is driven away from lactation towards body reserves. Further selection for age increased the proportion of EL (squares) and this allowed the trade-off between MILK and survival (arrow) to be overcome, because EL alleviated the pressure to maintain a high allocation towards body reserves to remain in the herd by avoiding the consequences of reproductive failure (Fig. 6). For these herds, the overall improvement in survival was slight, and this selection for age instead privileged high producing females (because of the selection weight on MILK), which caused the milk yield improvement. When the resource availability is limited in the environment, the resource allocation theory states that a trade-off between competing functions should occur at the individual level and that if the resource allocation has some genetic basis (as assumed in this model), the trade-off should also occur at the population level as a response to selection (Reznick, 1985; Stearns,1992). Figure 7 reveals indeed such a trade-off but also suggest that EL is an effective lever to alleviate it.

The bottom panel shows however that the positive effect of EL was not so apparent in terms of milk production efficiency, here approximated with the ratio between MILK and BW. The greater BW (Table 1) was explained by 2 effects, between generations and within animal lifetime. Between generations, selection with EL allowed some changes in the heritable component of the allocation that were not completely favourable to milk efficiency. Resource diverted away from body reserves were not fully reallocated to lactation (l_0 did not increase) but also to growth (i.e., non-labile BW) and survival. Within animal lifetime, the average BW was also increased (Fig. 3) mainly because of an innate increase in the resource acquisition of the dairy goat (Douhard et al., 2013). The control of this increase was apparently different to that involved just after parturition and might be a specificity of seasonal breeders such as goats (Linzell, 1973) and sheep (Jonas et al., 2011). It is clearly a key mechanism which contributes to the effectiveness of EL.

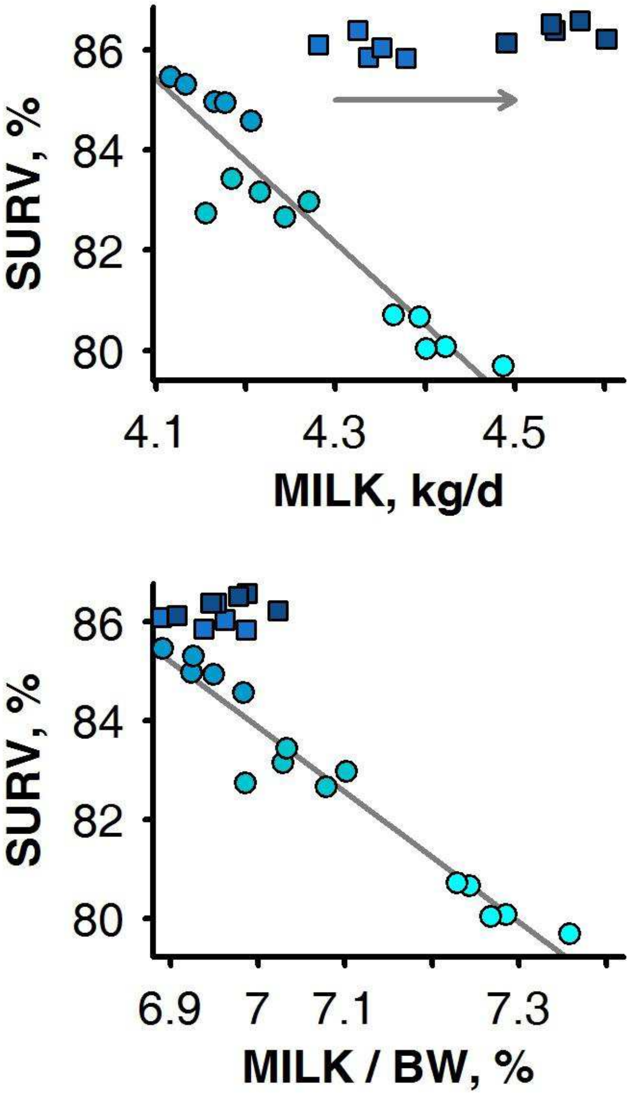

Figure 7: Relationships between the herd survival rate (SURV) and milk production, estimated as the average peak milk yield (MILK) alone or relatively to the average body weight (MILK / BW), when selecting for milk yield combined with an increasing emphasis for age (blue shading used in Fig. 5) in a variable environment (V-V scenario, see Material and Methods for scenario definition). High selection for age resulted in a high proportion of extended lactation (squares) compared to the others strategies (circles). Selection was practised during 40 years of selection and the last 5 years (20 replicates) are shown for each strategy.

Effect of environmental variability on robustness development

As shown in Fig. 8 and Table 2, a period of selection in a constant environment resulted in a survival rate always superior to that obtained in a variable environment, even when compared to the most robust genotype that emerged in the variable environment (dotted line: strategy W_{AGE} = 0.10 in V-V scenario). This latter strategy was assumed to be robust because it maintained the highest SURV and REPRO in the variable environment, through the heritable traits d_0 and l_0 rather than through EL. For the strongest values of W_{AGE}, the proportion of EL was high again and had an effect on BW, MILK and BCS. For clarity, the interaction between EL and W_{AGE} is presented in the next section so as to focus here on the genetic basis of robustness (i.e. when the proportion of EL was low; W_{AGE} = 0, 0.05 and 0.10).

In the K environment, response to selection were mainly driven by a decrease in the resource allocation to body reserves deposition (d_0) rather than by an increase in the allocation to lactation (l_0); resources were thus mainly reallocated to growth and survival (see Fig. 2). Females selected in the K environment were thus larger than those selected in the V environment (Fig. 8). Moreover, any increase in body size increases the resource acquisition capacity (R_G), so when the resource was available ad libitum, the resource obtained was increased, and so was MILK and SURV. Improvement in SURV was however limited with increasing selection for age because, independently of the nutritional conditions, the oldest females were more likely to die than young ones.

The selection for robustness in the V-environment was more successful in maintaining a constant SURV compared to the 2 strategies with a lower proportion of EL ($W_{AGE} \leq 0.10$ in K-V scenario). Some environmental variability during selection seemed thus to improve robustness development compared to just selecting for age and milk yield in constant conditions. Moreover, after 20 years of selection in the K or in the V environment, this same strategy (W_{AGE} = 0.10) had different outcomes (l_0 and d_0 panels in Fig. 8) but the values tend to converge thereafter, when herds are transferred in the V environment. This indicates that genetic variation maintained in the herd across years was enough to do so.

In the V environment, the high desired acquisition of large animals could not always be satisfied and this had a negative impact on SURV. The resource obtained from the environment and the body reserves and subsequently allocated to survival, was not always enough to compensate for the cost of maintaining a large body size. Therefore, after the transfer from K to V, BW tended to decrease towards an average value of BW that better fits with a variable resource availability and BCS tended to stabilize. With a low selection weight on age, these trends did not stop the decrease in SURV. There were 2 reasons for this. First, as MILK was still being selected for, this put more pressure on the resource allocation to lactation given the limited progress in resource acquisition (l_0, Fig 8), at the expense of survival (Van Der Waaij, 2004). Second, as BCS was not directly selected for in the different strategies, it was difficult to favour increased body fatness to better face variable conditions; d_0 was merely stabilized at the level obtained after the selection period in the K environment.

Such a result indicates that a genetic improvement in favourable condition is a risky strategy as it depreciates the need for body reserves while increasingly relying on the prevailing resource availability in the environment.

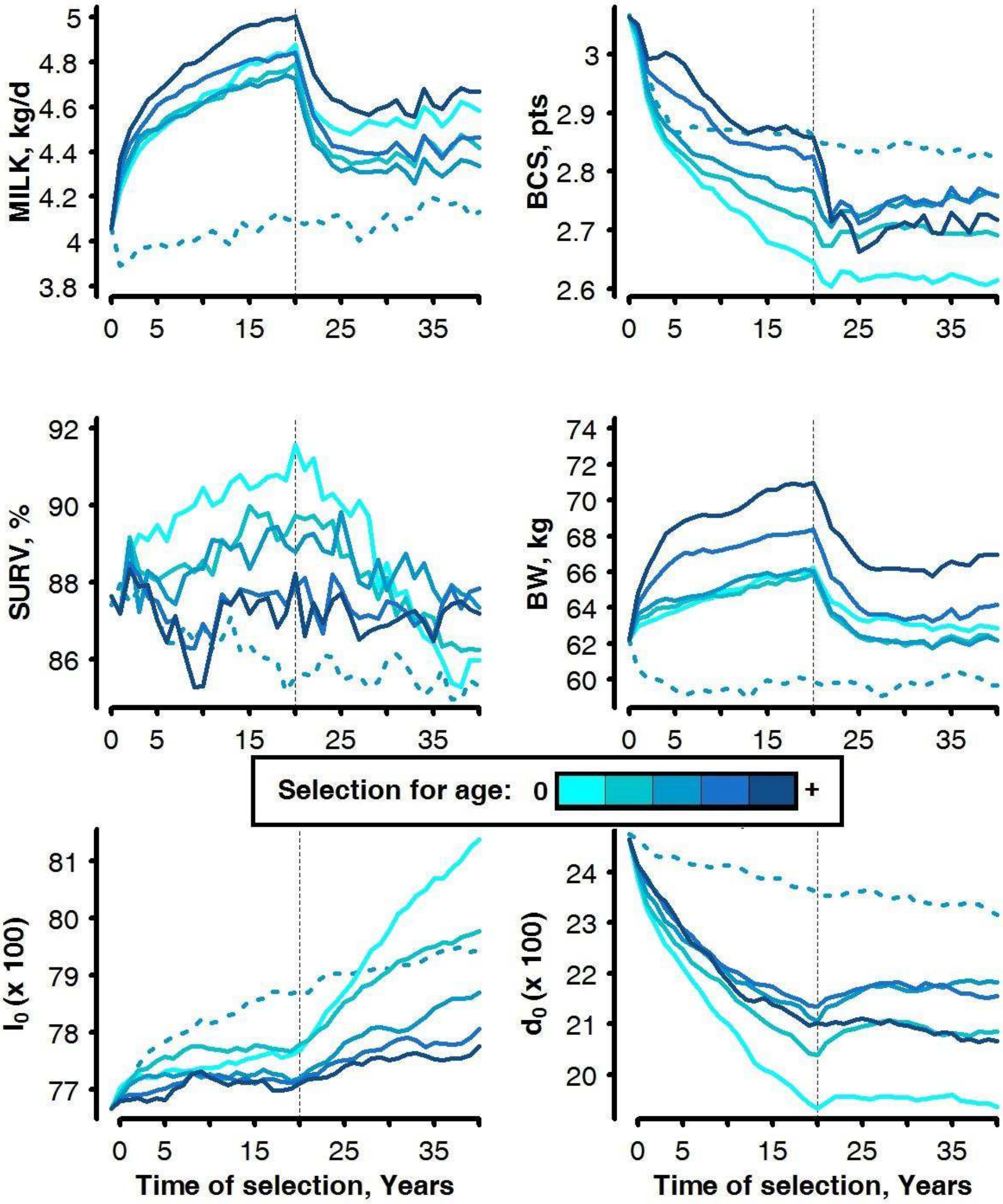

Figure 8: Responses in average individual performance to selection for milk yield and a different emphasis on age (blue shading) during 40 years in a herd provided with a constant resource availability for 20 years before being transferred in a variable environment (K-V scenarios). The dotted line indicates the response obtained when selection for age improves animal's robustness in a variable environment (W_{AGE} = 0.1 in V-V scenario, see Fig. 5). MILK: average peak milk yield. SURV and REPRO: survival and reproduction rate respectively.

Table 2: Performance means of simulated selection for milk yield and a different emphasis on age during 40 years in a herd provided with a constant resource availability for 20 years before being transferred in a variable environment (K-V scenarios). Means are calculated over the last 5 years of selection in each environment (K and V). Each selection strategy was replicated 20 times. MILK: average peak milk yield. SURV and REPRO: survival and reproduction rate respectively.

		Selection weight on age (W_{AGE})				
Variable	Environment	0	0.05	0.10	0.25	0.50
Milk, kg/d	K	4.83	4.76	4.72	4.82	4.99
	V	4.58	4.43	4.33	4.44	4.65
BCS, pts	K	2.66	2.73	2.77	2.83	2.87
	V	2.61	2.69	2.76	2.76	2.72
BW, kg	K	65.9	65.6	66.0	68.2	70.8
	V	62.9	62.3	62.2	63.9	66.7
SURV, %	K	90.9	89.5	89.1	87.7	87.5
	V	85.7	86.3	87.6	87.6	87.3
EL, %	K	0.5	1.0	2.6	7.6	12.7
	V	2.2	2.4	3.5	10.4	19.2

Interaction between EL and selection in alternated environments

Selection responses in the scenarios that used the K to V shift in environment were also dependent on the proportion of EL in the herd (Table 2). This was especially apparent in the BCS changes during the transfer from K to V. Average BCS decreased sharply for the 2 strategies with a high proportion of EL (i.e. $W_{AGE} \leq 0.1$) whereas it was maintained for the 2 others strategies (Fig. 8). In the K environment, the allocation traits under genetic influence (d_0 and l_0) were similar between W_{AGE} strategies that caused EL and the strategy which had the best SURV without causing EL ($W_{AGE} = 0.1$). This indicates that the high level of BCS in the K environment mainly resulted from the time-effects of body reserve deposition during EL rather than through a genetic reallocation to reserves. Therefore, the sharp BCS decrease observed after the transfer to the V environment resulted mostly from a body reserves mobilization within generation rather than from a genetic change in allocation between generations. In contrast, the decrease in BW resulted more from intergenerational effects; the large high producing females selected in the K environment could be kept within the herd, even if they failed to reproduce after their high body reserve mobilization. Their high resource acquisition allowed them to reach high MILK level in variable environment without putting too much pressure for an increase in l_0 which would compromise survival. Females born in the K environment could survive to the transfer but they were progressively replaced by others females with a similar genotypes. When they growth in the V-environment, these genotypes could not reach the mature BW they would have in the K-environment so BW was decreased. Still, EL allowed the maintenance of SURV between environments.

Fig. 9 shows that with increasing selection for age, EL had an effect to change trade-offs between MILK and SURV not only in the V environment (also observed in the V-V scenario; Fig. 7) but equally in the K environment (grey arrows, top left panel). Under favourable conditions, improvement in MILK based on EL resulted in less efficient animals than selection for MILK without EL animals in the herd (top right panel). This was mainly because resources are partly allocated to body reserves instead of to milk during EL. These extra body reserves allowed the maintenance of SURV in the V environment (dotted line, left panels). However, the trade-off between milk production and SURV was not as strong as observed in the V-V scenario (continuous grey lines, bottom panels). However, these trade-offs were not directly comparable as the number of generations selected in the V-environment was different and from different starting points.

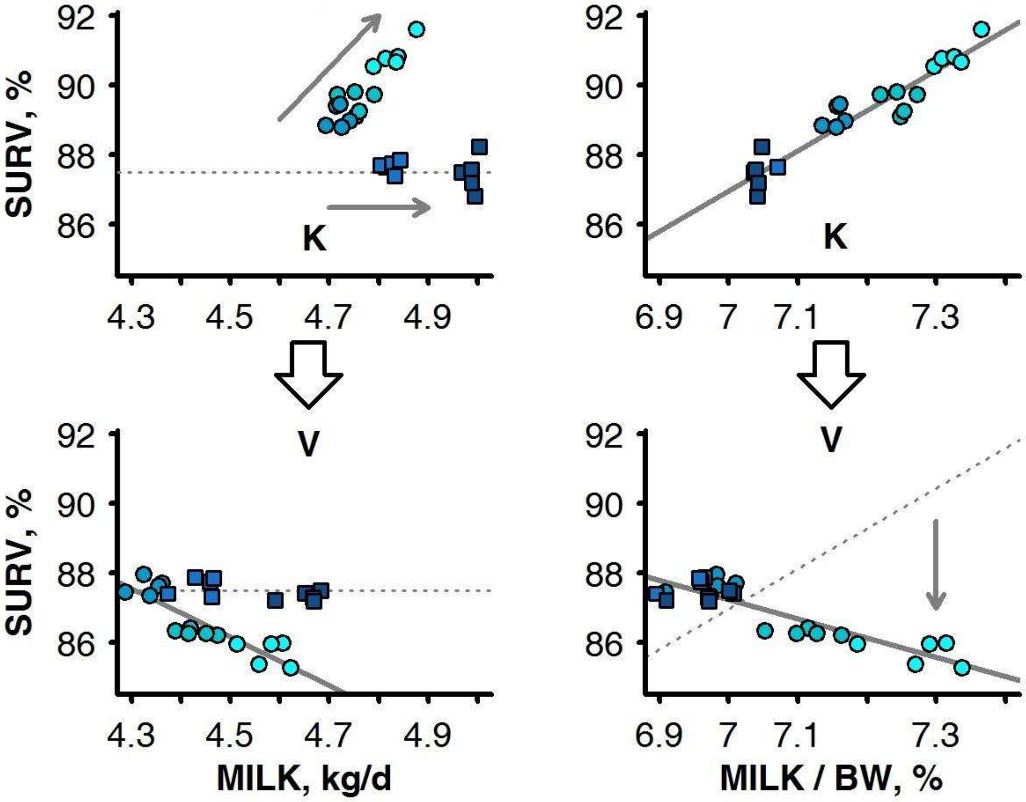

Figure 9: Effects of a transfer from a constant (K) to a variable environment (V) on the relationships between the herd survival rate (SURV) and milk production when selecting for milk yield combined with an increasing emphasis for age (blue shading used in Fig. 5). High selection for age resulted in a high proportion of extended lactation (squares) compared to the others strategies (circles). Milk production was estimated as the average peak milk yield (MILK) alone or relatively to the average body weight (MILK / BW). Selection was practised during 40 years (2 × 20 years) and the last 5 years (20 replicates) in each environment are shown for each strategy.

This study suggests that the combination of management (EL) and selection (for MILK and longevity) solutions represent a promising avenue to achieve robustness in dairy herds. The direct comparison of the 2 solutions could not be done from the reported simulation experiments because females that were undergoing EL were also those selected for longevity (i.e. EL was a correlated response to W_{AGE}). In practice, farmers do not reserve the use of EL only to the oldest females. In some dairy goat situations, they even do the contrary as they deliberately do not put primiparous females to reproduction to leave them recovering from the metabolic stress of their first parturition. As these females are still growing the increase in resource acquisition during EL may enhances growth and allow achieving a greater mature size. The gain in live weight would promote size and thus the acquisition potential rather than fatness so the low efficiency of EL suggested for multiparous (Fig 9) might be improved. However, a greater desired is associated with greater environmental sensitivity (Douhard et al., in prep). Further investigation would be required to assess the insurance role of EL with goats that are deemed to be more vulnerable because of their genotype or of their stage of development, or both. However, this would also require further characterization of EL, in particular for primiparous.

Modelling is a powerful tool to highlight the consequences of a biological phenomenon still little explored such as EL (Rotz et al., 2005). The main originality of our model was to combine the selection and the production process at the herd level. In particular, this helped to shed light on the modulation of biological effects through a management practice. Still, the interest and the feasibility of this practice in the herd system depend on much more factors than the biological responses. In particular, it would be desired to account for the economics of EL in a particular feeding system. In a pasture-based system where the feed costs are relatively low compared to those of replacing females, one could hypothesize that the lower efficiency of EL is not prohibitive. For such complex issues, a model which accounts for the management priorities would be highly desired to explore the innovative potential of EL for the design of herd systems addressing the need to adapt to their global environment.

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COMPLEMENTARY PART

(Ph.D. summary in French)

Vers des systèmes d'élevage résilients : une approche de l'allocation de la ressource pour combiner sélection et conduite dans l'environnement du troupeau

Introduction

Sélectionner les animaux qui ont le plus haut niveau de production, en tenant peu compte d'autres traits de caractères, a toujours bien fonctionné dans les conditions d'un environnement favourable (i.e. ration riche en nutriments, faible charge pathogène, thermoneutralité). Les évolutions récentes du contexte de production laissent penser que les éleveurs auront de plus en plus de mal à réunir ces conditions dans l'environnement de leur troupeau (Thornton, 2010; Nardone et al., 2010). Dans un contexte marqué par l'incertitude, les conditions locales du troupeau représentent alors une voie d'entrée privilégiée pour identifier les moyens de mettre en place des modes de production durables dans les systèmes d'élevage (Gibon et al., 1999; Darnhofer et al., 2008), notamment en cherchant à valoriser les capacités d'adaptation des animaux à leur milieu (Provenza, 2008; Peyraud et al., 2009). Du point de vue du troupeau, le choix d'un matériel génétique adapté repose non seulement sur des critères d'efficacité de la production mais également sur des critères fonctionnels (i.e. ceux qui permettent d'assurer le bon fonctionnement du troupeau en dépit de perturbations exogènes). De ce point de vue, plusieurs éléments permettent actuellement de pointer le risque d'un matériel génétique inadapté.

Lorsque la performance des animaux est mesurée par rapport l'expression d'un niveau de production, les génotypes les plus performants sont souvent les mêmes quelque soit l'environnement (Veerkamp et al., 2009). L'absence de reclassement dans différents environnement suggère que ces génotypes performants sont aussi adaptés. Ainsi, il n'y a nul besoin de considérer une interaction entre les génotypes et leur environnement dans les schémas de sélection. Ce besoin est plus évident, lorsque la capacité d'adaptation est évaluée par rapport une performance multiple. Si cette performance multiple pouvait être résumée en un seul critère (i.e. survie, production, reproduction) alors une façon schématique de représenter les effets de la sélection revient parfois à distinguer des génotypes spécialistes (capables d'exprimer un haut niveau de performance mais sur une gamme étroite de contraintes environnementales) par opposition aux généralistes (capables d'exprimer un niveau de performance plus modeste mais sur une gamme plus étendue de contraintes) (Bryant et al., 2006; Strandberg, 2009). En pratique, une telle distinction semble en effet valable pour un grand nombre d'espèces domestiques sélectionnées (Rauw et al., 1998; Olesen et al., 2000). En particulier, les effets de la sélection en ruminants laitiers confirment assez largement l'hypothèse d'une spécialisation. D'une part l'augmentation spectaculaire du niveau de production s'associe à une tendance à la baisse de la fertilité (Lucy, 2001; Walsh et al., 2011). D'autre part, des corrélations génétiques négatives sont souvent mesurées entre la production de lait, et la fertilité et la santé (e.g. Pryce et al., 1997). Par conséquent, sur le long terme la sélection semble s'approcher d'une situation où toute augmentation de la production laitière compromet les chances de reproduction et de survie de l'espèce, autrement dit une situation où un compromis évolutif (ou « trade-off ») devient apparent (Rauw et al., 1998).

Les notions de spécialistes/généralistes font aussi écho à la capacité d'adaptation des animaux du point de vue de la nutrition dans les troupeaux. Au fur et à mesure des générations, la sélection des animaux pour générer des gains d'efficacité à court-terme affecte le partage des nutriments ingérés, par exemple en augmentant la part vers le lait chez les espèces laitières (Veerkamp, 1998; Friggens and Newbold, 2007). Lorsqu'au cours de leur vie ces animaux spécialisés pour la lactation ne peuvent ingérer suffisamment d'aliments pour couvrir leurs besoins nutritionnels élevés, leur capacité à réajuster leur partage en faveur d'autres fonctions biologiques apparait génétiquement limitée (Ingvartsen et al., 2003). Le déficit nutritionnel conduit à une mobilisation accrue des réserves corporelles (Chilliard et al., 1998) et éventuellement à une réduction de la vie productive soit par un effet direct sur la survie (mortalité et réforme sur problèmes de santé), soit par un effet indirect via la reproduction (réforme sur infertilité). Dans un contexte de production plus en plus variable, le risque associé à la spécialisation semble considérable dans les troupeaux. Sur le plan technique et économique les difficultés maintenir un environnement nutritionnel riche et abondant s'accroissent (Lelyon et al., 2011) tandis que sur le plan biologique la gamme de contraintes nutritionnelles pour maintenir l'expression des traits de caractères fonctionnels s'amenuise. Sélectionner des animaux compatibles avec les conditions futures des troupeaux devient donc tout aussi important qu'adapter la conduite du troupeau en fonction des génotypes sélectionnés par le passé.

Deux grandes voies peuvent-être envisagées pour sélectionner des animaux adaptés à leur environnement de production. Une première voie explorée par les généticiens consiste à ajuster les critères utilisés dans les schémas de sélection (sélection multicritère, prédiction des réponses à la sélection dans un environnement de troupeau identifié) (Veerkamp et al., 2009). Cette voie implique néanmoins toujours d'avoir suffisamment de données pour estimer précisément les paramètres utilisés dans les prédictions (Kolmodin et al., 2002), ce qui pose problème lorsqu'un environnement de troupeau est trop spécifique pour être suffisamment renseigné (Windig et al., 2006). Malgré ces difficultés, cette voie semble prometteuse pour aider les éleveurs à mieux décider du matériel génétique qu'ils importent dans leur troupeau, en fonction des conditions particulières de leur élevage (Huquet et al., 2012a). De ce point de vue, il semble crucial d'examiner attentivement le rôle de l'éleveur qui définit les critères et la stratégie de sélection employée dans le troupeau et module ou non l'environnement pour favoriser l'expression génétique des animaux à travers le temps. Une seconde voie consiste à aborder le problème à l'échelle du système d'élevage (Bryant et al., 2008). Du point de vue de l'éleveur, le problème s'apparente plus à la recherche d'une combinaison satisfaisante entre les objectifs de sélection et la conduite plutôt qu'à l'optimisation du progrès génétique dans le troupeau. L'originalité de cette voie apparemment peu explorée à ce jour est de pouvoir exploiter les interactions G × E (plutôt que de les minimiser) et avec d'autres moyens que seulement la sélection génétique, c'est-à-dire agir à la fois sur 'G' et sur 'E'. Néanmoins, l'identification de ces moyens ainsi que les contraintes et les opportunités pour leur mise en œuvre requièrent une intégration des réponses à la sélection et des réponses à la nutrition. Or, la prédiction de ces réponses est abordée de façon très distincte (Bryant et al., 2005).

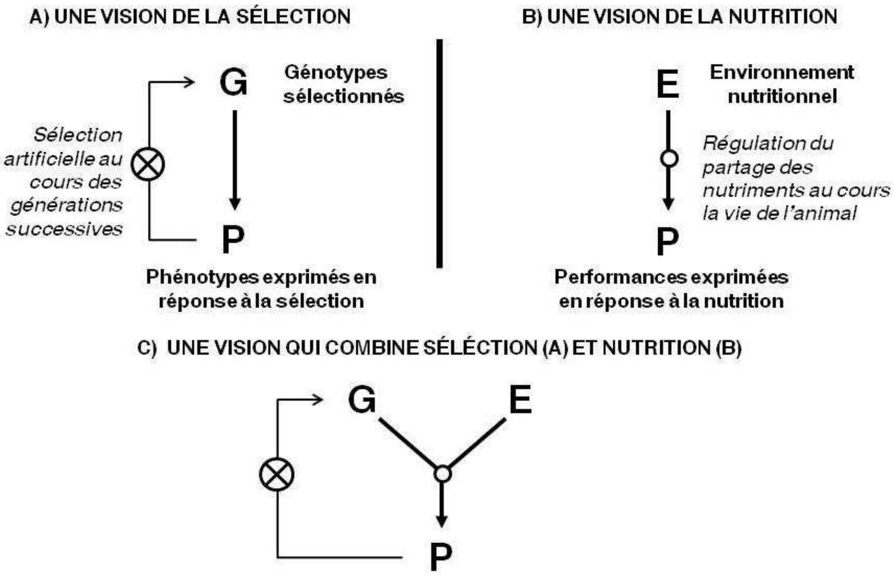

Figure 5 : Deux visions séparées et simplifiées de la sélection (A), vue comme un processus intergénérationnel visant à sélectionner les individus supérieurs dans une population et de la nutrition (B), vue comme un processus intragénérationnel grâce auquel l'individu transforme les nutriments ingérés de façon à couvrir les besoins de ses performances multiples. L'émergence d'interactions génotypes-environnement peut-être vue comme le résultat des deux processus (C).

La modélisation est un outil puissant pour intégrer les relations complexes entre les facteurs génétiques, l'environnement nutritionnel et le temps (McNamara, 2012). Cependant, l'approche prédictive distincte de la nutrition animale et de la sélection génétique tient sans doute au fait que les processus impliqués opèrent à des échelles spatiales et temporelles très différentes.

La prédiction des réponses à la sélection sert à identifier les génotypes supérieurs qui seront choisis pour être parents/géniteurs dans une population nationale ou régionale, et à réitérer le processus au cours des générations successives (Figure 5A). La prédiction des réponses nutritionnelles quand à elle s'opère à l'échelle de l'individu dans le troupeau et sur des pas de temps courts en fonction notamment du stade physiologique des animaux (Figure 5B). La régulation dynamique et coordonnée des réponses nutritionnelles par des facteurs génétiques est bien reconnue (Bauman and Currie, 1980; Chilliard, 1986; Friggens et al., 2013). Théoriquement, cette composante devrait donc être héritée entre générations. L'expression des performances au cours de la vie des animaux conditionne à son tour la réponse à la sélection dans le troupeau, notamment par le biais des taux de réforme (reproduction et survie). Une vision qui combine les deux processus semble souhaitable pour décrire leur interaction et identifier les moyens d'exploiter les interactions G × E dans le troupeau (Figure 5C). Pour faire face à une telle complexité, la modélisation nécessite une base théorique permettant d'intégrer les effets de la sélection et de la conduite du troupeau à court terme (i.e. variabilité hebdomadaire du niveau d'alimentation) et à long terme (i.e. transmission de traits de caractères entre générations).

La théorie de l'allocation des ressources développée en biologie évolutive postule que les individus acquièrent une quantité de ressources limitée dans leur environnement, de telle sorte que la sélection naturelle favorise les animaux qui allouent cette ressource de façon optimale entre les fonctions de survie, reproduction et croissance (Williams, 1966; Stearns, 1992). Autrement dit certaines stratégies d'allocation conduisent à une meilleure valeur sélective (ou « fitness ») au cours de l'évolution. Deux aspects de la théorie permettent de faire une analogie avec la sélection des animaux domestiques. L'une est reflétée dans les termes «allocation» et «partage», qui sont effectivement synonymes (Friggens and Newbold, 2007). L'autre aspect réside dans le parallèle entre la valeur sélective et l'index de sélection utilisés dans la sélection artificielle, car tous deux reflètent une mesure d'adaptation des individus à leur environnement (mais avec une pondération différente des traits de caractères, Mignon-Grasteau et al. (2005)). L'importation du principe d'allocation de la ressource dans le cadre des animaux domestiques (Beilharz et al., 1993; Rauw, 2009) n'est pas directe car la domestication a considérablement repoussé les limites imposées par l'environnement sur la quantité de ressource obtenue (à la fois par l'amélioration de la disponibilité et par la réduction de l'effort fourni par les animaux pour s'alimenter). D'après la théorie de l'allocation adaptée par Beilharz et al. (1993), un compromis évolutif entre traits ne doit apparaitre que si le progrès génétique devient limité par la quantité de ressource fournie par l'environnement. Cela peut-être illustré avec un modèle simplifié de l'individu (i.e. un organisme) dans une population (van Noordwijk and de Jong, 1986; Van Der Waaij, 2004) (Figure 6). Si les individus acquièrent une quantité de ressource limitée dans leur environnement (R) et l'allouent entre deux fonctions (1 et 2), alors la sélection pour un caractère d'intérêt (e.g. P_1) favorise les animaux qui allouent une quantité plus importante de ressource (R_1) pour exprimer ce caractère (i.e. les animaux dont l'allocation c (entre 0 et 1) est la plus élevée possèdent la plus grande valeur sélective). Si en outre une part de la variation interindividuelle de l'allocation c est d'origine génétique alors la population doit répondre à la sélection au fur et à mesure des générations (Reznick, 1985; Stearns, 1992). Autrement dit, la moyenne phénotypique de c doit augmenter de même que celle P_1 tandis que celle P_2 doit diminuer, révélant ainsi un compromis évolutif entre P_1 et P_2 (Figure 6A). Si par contre au cours des générations successives, l'environnement permet d'accomplir les progrès pour P_1 par une augmentation de la capacité d'ingestion (R) plutôt que par un changement d'allocation de la ressource, alors aucun compromis évolutif ne doit apparaitre (Beilharz et al., 1993; Beilharz and Nitter, 1998) (Figure 6B). Bien que ces principes soient établis à partir d'un modèle simple d'allocation entre deux fonctions et sur un pas de temps générationnel, ils constituent une base théorique pour connecter les effets de la sélection génétique et les effets de la conduite sur la nutrition.

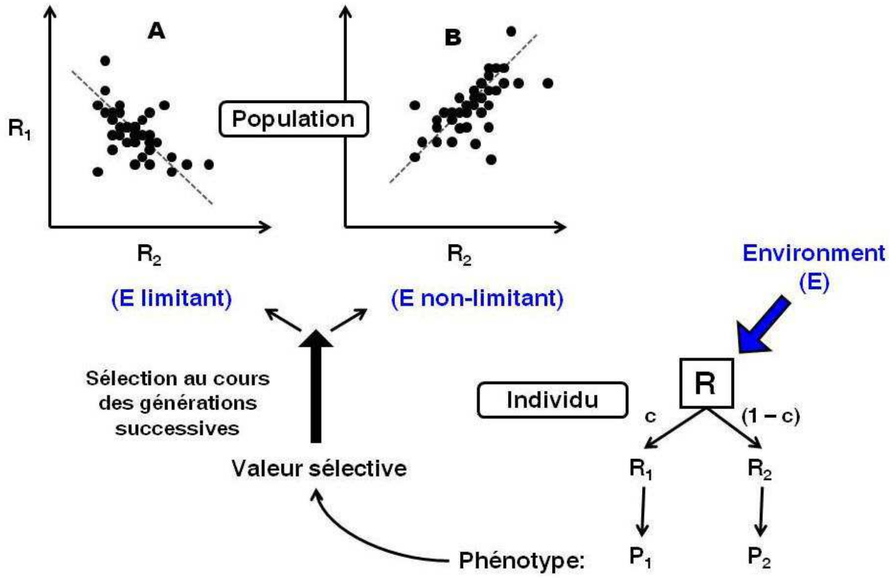

Figure 6 : Un modèle de base d'allocation de la ressource entre deux fonctions au niveau de l'individu (en bas à droite) et les conséquences de la sélection au niveau populationnel selon deux scénarios de contraintes environnementales

La conduite du troupeau peut difficilement se résumer à la simple mise à disposition d'une quantité de ressource. D'une part, les animaux expriment des besoins variables au cours de leur vie, notamment en fonction de leur stade physiologique. D'autre part, la quantité de ressource obtenue ne provient pas seulement directement de l'environnement mais également des réserves corporelles. Enfin, la sélection des animaux dans le troupeau s'opère par le biais des pratiques de réforme et de renouvellement de telle sorte que les générations ne se succèdent pas mais se chevauchent. En pratique, les stratégies de conduite du troupeau s'appuient activement sur ces éléments (gestion de différents stades reproductifs, utilisation des cycles de mobilisation-reconstitution des réserves corporelles, définition des choix de réforme-renouvellement) ce qui laisse penser qu'ils constituent des leviers d'action importants pour améliorer la situation de compromis telle qu'elle est décrite simplement en Figure 6A.

Objectif de recherche et démarche

Dans cette thèse, nous proposons que l'exploitation des interactions G × E au niveau du troupeau nécessite une représentation l'animal qui intègre à la fois les effets de la sélection et les effets de la conduite du troupeau sur la nutrition. L'introduction nous a permis de montrer l'intérêt potentiel d'une telle intégration mais également le défi conceptuel que cela représente. Pour relever ce défi, nous avons choisi de partir du principe selon lequel la sélection et la conduite du troupeau influencent la façon dont chaque animal alloue ses ressources entre ses fonctions biologiques. Le choix du principe d'allocation s'appuie à la fois sur 1) son utilisation considérable dans le domaine de la biologie évolutive (Stearns, 1992), 2) son potentiel explicatif dans le cadre de la sélection des animaux d'élevage (Beilharz et al., 1993; Rauw, 2009), et 3) sur son application dans un modèle simple pouvant servir de point de départ pour connecter les effets de la sélection et les effets de la conduite du troupeau sur la nutrition (Van Der Waaij, 2004). Dans cette thèse, nous avons cherché à évaluer la portée du principe d'allocation de la ressource pour mieux comprendre le développement des interactions génotype-environnement (G × E) dans un troupeau sur le long terme.

Pour parvenir à cet objectif, nous avons cherché à décrire l'animal (et son génotype) en termes d'allocation puis à intégrer cette description dans un modèle individu-centré. Notre évaluation se base alors sur la capacité du modèle d'une part à générer des prédictions cohérentes par rapport à la réalité observée, et d'autre part à éclairer les mécanismes impliqués dans le développement des interactions G × E. Le modèle animal a été développé et calibré en chèvre laitière mais avec une représentation qui semble suffisamment stylisée pour envisager une comparaison avec d'autres espèces de ruminants pour lesquels les conséquences de la sélection sont mieux renseignées (bovin laitier notamment). Comme ici le terme 'E' de G × E ne fait pas seulement référence à un niveau de la disponibilité de la ressource mais à l'environnement de troupeau résultant de la conduite, nous avons cherché à représenter les effets d'un levier technique en particulier. Nous nous sommes concentrés sur la conduite de la lactation longue

(LL) chez la chèvre laitière qui suscite un intérêt croissant dans les élevages, notamment pour compenser les échecs de reproduction, mais qui reste un phénomène biologique peu connu notamment sur le plan de l'allocation de la ressource entre fonctions.

La démarche que nous avons suivie pour répondre à l'objectif de recherche se décompose en trois sous-questions (reportées en Figure 7):

i. Quels sont les effets à long terme de différentes stratégies de sélection sur les performances du troupeau obtenus à partir du modèle animal d'allocation de la ressource ?

ii. Quelle est l'allure du profil temporel de la performance au cours de la lactation longue et comment l'intégrer dans le modèle animal proposé ?

iii. Quels sont les effets simulés d'une interaction entre différentes stratégies de sélection et l'utilisation de la lactation longue dans les troupeaux soumis à des variations de l'environnement nutritionnel ?

L'approche générale utilisée est adaptée de celle proposée par Giller et al. (2008) qui situe les différents rôles de la modélisation pour éclairer la valeur d'un concept dans un processus de recherche. Le modèle présenté dans cette thèse se situe à mi-chemin entre les modèles simples utilisés pour illustrer le potentiel explicatif d'une théorie (par exemple Van Der Waaij , 2004) et ceux qui ont été conçus et calibrés pour faire des prédictions plus précises dans le monde réel (par exemple, Fox et al. , 2004). Il comprend trop de composants pour être facilement analysé dans le premier cas et présente un niveau de simplification trop important pour le second cas. Sa complexité et le niveau de description de ses composantes ont été déterminés pour favoriser l'exploration de scénarios.

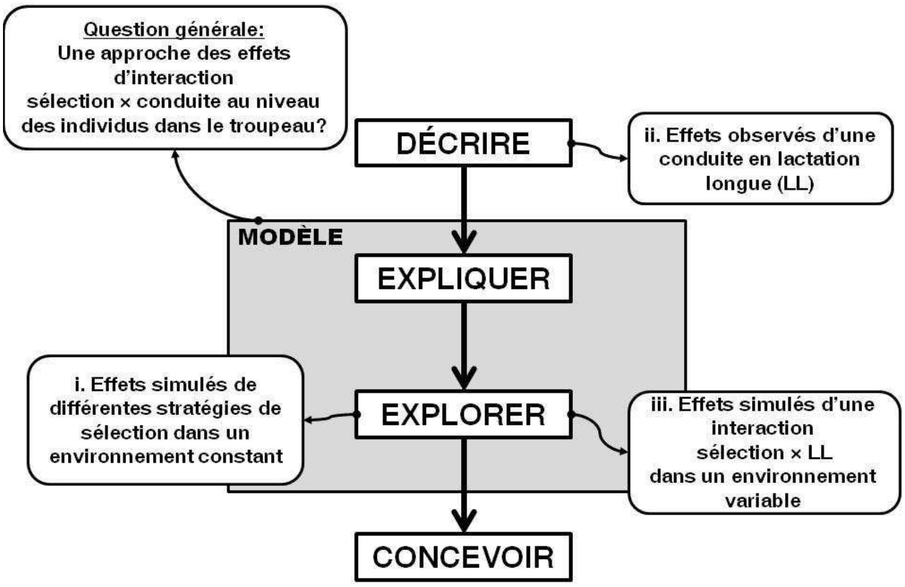

Figure 7 : Approche générale de la thèse (adaptée de Giller et al. (2008)) suivie pour répondre aux sous-questions de recherche

Approche générale de la thèse

Expliquer les effets de la sélection dans le troupeau sur les performances

Les principaux processus qui composent le modèle de simulation du troupeau développé dans cette étude sont présentés en Figure 8. Le modèle est individu-centré, implémenté en temps discret et combine un pas de temps hebdomadaire (cycle de gauche) pour l'alimentation, avec un pas de temps annuel (cycle de droite) pour la sélection et la mise à la reproduction des animaux.

Le point clé reliant les deux cycles est la description du génotype de chaque individu du troupeau par des caractéristiques héritables (T_1, T_2, T_3 ...). Comme ce sont des caractéristiques de l'allocation de la ressource, elles conditionnent les réponses nutritionnelles des individus et leur performance hebdomadaire. Cette performance multiple (P_1, P_2, P_3 ...) est enregistrée pendant l'année n-1 pour définir les critères de sélection des individus choisis pour être parents l'année suivante n. Cette performance décrit non-seulement des traits de caractères zootechniques (lait, poids, note d'état corporel…) mais détermine aussi les chances de conception et de survie. Par ailleurs, au cours du processus d'accouplement, les parents sélectionnés transmettent leurs caractéristiques héréditaires (T_1, T_2, T_3 ...) à leur descendance. Chaque année, les individus ayant survécu sont évaluées à partir 1) de certains critères de leur performances annuelle observée, et 2) de l'importance relative (W_1, W_2, W_3 ...) de chacun de ces critères pour l'éleveur. Ces deux informations sont combinées individuellement dans un index de sélection (SelIndex) permettant de classer les candidats et de les sélectionner:

$\text{SelIndex} = (W_1 \times P_1) + (W_2 \times P_2) + (W_3 \times P_3) + \ldots$

Chaque année, une proportion constante des meilleurs candidats (ceux dont la valeur SelIndex est plus élevée) désigne ceux qui sont sélectionnés en tant que parents tandis que la proportion restante est volontairement réformée et remplacée avec une partie de la descendance née pendant l'année. Ici, les individus immatures choisis pour renouveler le troupeau sont issus des meilleures mères (sélection sur ascendance). Par ailleurs, les mâles utilisés pour la reproduction sont issus du troupeau et remplacés chaque année (i.e. système fermé). Dans l'ensemble, ce sont donc les choix de sélection de l'éleveur et les variations inhérentes des taux de reproduction et de mortalité qui permettent de générer le progrès génétique dans le troupeau.

Dans le modèle, nous avons limité la nature de la ressource nutritionnelle à l'énergie métabolisable d'un aliment standard et d'une qualité constante. Le sous-modèle animal permet d'exprimer pour chaque semaine la quantité de cette ressource que chaque animal désire. A chaque pas de temps, la proportion P_{LIM} (entre 0 et 1) des animaux qui peuvent complètement satisfaire leur niveau de ressource désiré a été utilisée comme une donnée d'entrée du modèle pour définir le niveau disponibilité de la ressource dans l'environnement (R_E).

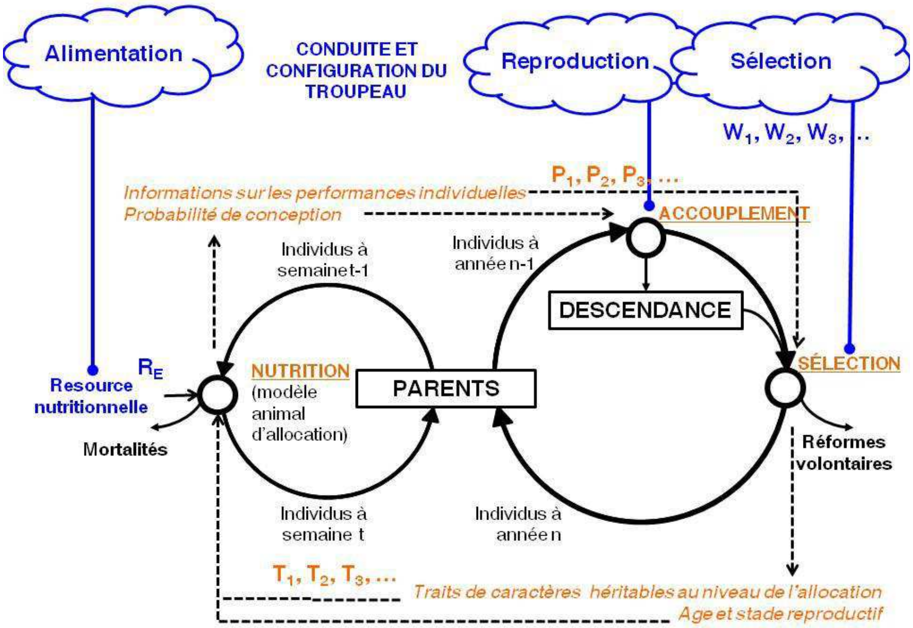

Figure 8 : Vue d'ensemble des trois processus constituant le modèle de simulation de troupeau (nutrition, accouplement et sélection) et de leur connexion avec la démographie et la conduite du troupeau

Le sous-modèle animal procède en deux étapes, 1) l'acquisition de la ressource à partir de l'environnement, et, éventuellement des réserves corporelles, puis 2) l'allocation de cette ressource acquise entre les fonctions biologiques.

La formalisation de l'acquisition s'appuie sur la notion d'un niveau d'ingestion désiré. Cette notion permet de considérer de façon simplifiée que la capacité d'ingestion de l'animal est liée à sa taille (estimée dans le modèle par le poids vif non-labile) et que l'animal régule de façon son niveau d'ingestion en fonction de son état d'engraissement (Tolkamp et al., 2006, 2007). Cette régulation s'opère par rapport à une proportion de réserves corporelles ciblée et défendue de façon innée par l'animal (Kennedy, 1953) de telle sorte qu'un excès de réserves réduit le niveau d'ingestion et qu'un déficit l'augmente (Tolkamp et al., 2006). Le point clé de la formalisation de l'acquisition dans le modèle est que ce niveau d'ingestion désiré à un temps t dépend de l'état de l'animal au temps précédent t -1. Cet état (note d'état corporelle et poids vif non-labile) est quand à lui déterminé par l'allocation de la ressource acquise entre les différentes fonctions.

L'allocation de la ressource est le point central du modèle puisque c'est à ce niveau que sont présumées les caractéristiques héritables de l'animal (T_1, T_2, T_3 ...). Pour représenter une hiérarchie d'allocation entre les principales fonctions biologiques d'un ruminant laitier (réserves corporelles, gestation, lactation, croissance et survie), nous avons étendu le modèle d'allocation entre deux traits décrit en Figure 6. Pour chaque niveau de la hiérarchie, nous avons préservé le même principe à savoir qu'une proportion (c) de la ressource est allouée à une fonction tandis que la proportion restante (1 – c) est disponible pour l'allocation aux niveaux suivants (Figure 9). Cette allocation c est décrite avec une lettre différente dans la hiérarchie présentée (d, p, l et g) et chacune d'entre elles suit un modèle général qui combine trois composantes d'allocation dont la valeur reste comprise entre 0 et 1 ;

$c = c_0 \times cmod_G \times cmod_E$,

c_0 est une valeur constante durant la vie de l'individu, $cmod_G$ est une fonction représentant la modification des priorités d'allocation au cours de sa vie, enfin $cmod_E$ est une fonction représentant la modification de l'allocation pour faire face aux variations du niveau de ressource obtenue dans l'environnement. Lorsque le niveau de satisfaction de la ressource désirée baisse, alors la valeur de $cmod_E$ baisse aussi (donc celle de d, p, l et g) de telle sorte que la ressource obtenue (Robt) est réallouée vers la survie. D'une façon simplifiée, le produit $c_0 \times cmod_G$ représente donc les régulations de téléophorèse de l'allocation tandis que $cmod_E$ représente celles d'homéostase (Sauvant, 1994; Martin and Sauvant, 2010). Ces deux types de régulations ont aussi été considérés pour représenter la mobilisation des réserves corporelles (Rmob). Ainsi une partie des réserves est mobilisée indépendamment de l'environnement après la mise-bas, tandis qu'une autre partie peut aussi être mobilisée lorsque le niveau de satisfaction de la ressource désirée baisse (Friggens et al., 2004). Les paramètres du modèle animal ont ensuite été calibrés à l'aide d'un profil temporel de performance de chèvre laitière dans un milieu nutritionnel favorable.

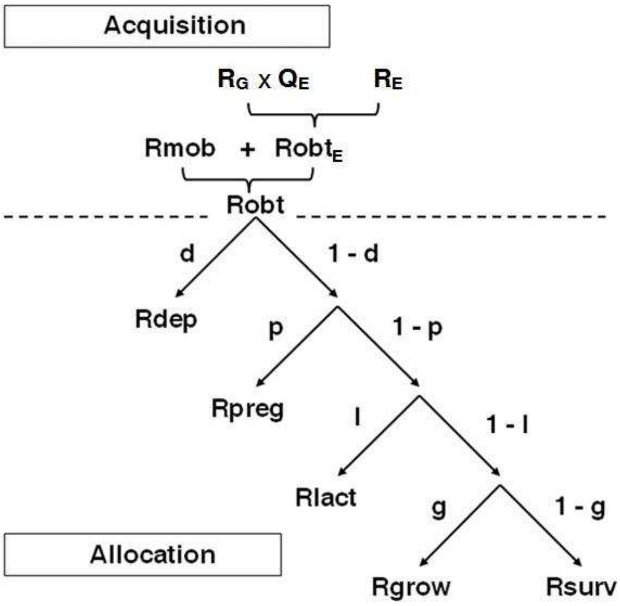

Figure 9 : Représentation schématique de l'acquisition et de l'allocation de la ressource dans le sous-modèle animal. R_G : niveau d'ingestion désiré, Q_E : qualité de la ressource (entre 0 et 1), R_E : quantité de ressource disponible dans l'environnement, Robt$_E$: ressource obtenue de l'environnement, Rmob : ressource obtenue par mobilisation des réserves corporelles, Robt : ressource totale obtenue, d,p l et g : coefficients d'allocation de la ressource (entre 0 et 1) pour le dépôt de réserves corporelles, la gestation, la lactation et la croissance respectivement. Lorsqu'au cours la vie de l'animal la contrainte nutritionnelle augmente la valeur ces coefficients sont réduits de façon à favoriser une réallocation de la ressource vers la survie.

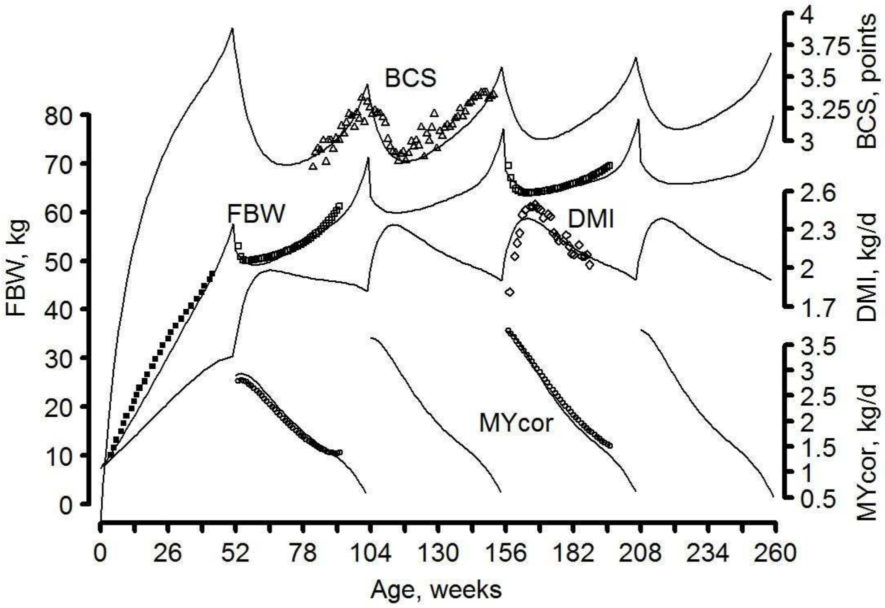

Figure 10 : Données simulées (lignes continues) des variations de note d'état corporelle (BCS), de poids vif (FBW), de matière sèche ingérée (DMI) et de la production de lait standard (MYcor) au cours de la vie de l'animal depuis sa naissance jusqu'à 5 ans (soit 260 semaines). Les symboles représentent les données

utilisées pour la calibration du modèle: Sauvant et al, 2012 (○ et □); Puillet, 2010 (■); Sauvant et Morand-Fehr, 1982 (◊); Douhard et al, données non publiées (Δ).

Décrire le profil temporel de la performance au cours la LL

Pour mieux compléter le profil temporel de performance de la chèvre laitière en cours de LL, certaines données étaient disponibles dans la littérature (Linzell, 1973a; Chastin et al., 2001; Salama et al., 2005) mais aucune d'entre elles ne nous a permis de faire d'hypothèse à propos de l'allocation de la ressource entre fonctions. En revanche, la courbe de lactation observée dans chacune de ces études suggérait l'implication d'un mécanisme particulier sans que cela ne soit détaillé. Nous avons alors conduit une étude expérimentale pour comparer les effets de la LL avec une lactation normale (LN ; environ 300 jours de lactation) et pour caractériser les relations entre la production laitière, le poids vif et l'ingestion associés avec le profil temporel de la LL (Douhard et al., 2013). Cette caractérisation a notamment pu permettre d'identifier laquelle parmi les variables zootechniques semble entrainer les autres pour pouvoir envisager le mécanisme impliqué lors de la LL.

Explorer différents scénarios de sélection et de conduite

Paramétrage de G : les caractéristiques d'allocations sous influence génétique (T_1, T_2 ...) ont été considérées au niveau des coefficients d'allocation pour le dépôt de réserves corporelles (d) et pour la lactation (l), plus précisément au niveau de la composante de ces allocations qui reste constante au cours de la vie de l'animal (d_0 et l_0 respectivement). Pour simuler la valeur génétique de ces composantes, nous avons supposé que les paramètres génétiques classiquement requis étaient égaux à ceux estimés lors la calibration sur le méta-profile (une moyenne phénotypiques, ici de 0,25 et 0,75 respectivement pour d_0 et l_0, un écart-type phénotypique de 0,05 pour chacun et une héritabilité de 0,3 pour chacun). Les valeurs génétiques initiales ont été simulées dans une population de base et celles de tout nouvel individu ont ensuite été simulées à partir de celles de ses parents.

Paramétrage de E : Deux types d'environnements nutritionnels ont été définis. Dans un environnement constant et abondant, 100% des animaux étaient nourris ad libitum n'étant alors limité que par la qualité élevée et constante de la ressource. Dans un environnement variable, la disponibilité de la ressource R_E varie à la fois intra-année et inter-années. Pour chaque année, la proportion moyenne d'animaux nourris ad libitum a été déterminée de façon stochastique dans une loi uniforme (comprise en 25% et 100%). Une variation hebdomadaire du niveau de ressource autour de la moyenne annuelle a également été simulée à partir d'une loi normale.

***Scénarios G × E** :* Dans cette synthèse, nous reportons les effets de trois critères (P_1, P_2, P_3 …) dans l'index de sélection : le lait au pic (MILK), le poids vif moyen pendant l'année (BW) et l'âge de l'animal au moment de la sélection (AGE). Les paramètres reflétant l'importance de ces critères pour l'éleveur (W_1, W_2, W_3, ...) ont permis de paramétrer les scénarios testés (Tableau 2). Les résultats issus de deux types de scénarios sont reportés en lien avec les questions de recherche i) et iii) (Figure 7). Dans un environnement constant et abondant, nous avons testé les effets d'une sélection pour la production laitière uniquement puis avec différents niveaux de pénalisation pour le poids vif. Cette pénalisation est fréquemment utilisée dans les index de sélection en situation d'élevage intensif pour favoriser une efficacité productive (Veerkamp, 1998). Dans un environnement variable, nous avons testé les effets d'une sélection pour la production laitière uniquement puis avec différents niveaux de sélection pour l'âge. En outre, dans ce scénario nous avons permis l'utilisation de la LL (contrairement au scénario précédent où une réforme stricte sur infertilité a été simulée). Pour cela, nous avons inclus un $4^{\text{ième}}$ critère renseignant le statut reproductif de la femelle (gestante ou non). Ainsi, à la suite d'un échec à la reproduction les femelles non-gestantes peuvent être conduite en LL si elles font parties des candidats sélectionnés. Les femelles ayant une production élevée et étant éventuellement âgées sont ainsi favorisées.

Tableau 2 : Scénarios de sélection simulés. La stratégie de sélection est définie selon l'importance donnée aux différents critères de l'index de sélection (Voir détails dans le texte)

	Stratégie de selection			**Lactation longue (PREG)**
Environment	+AGE	**MILK**	-BW	
Constant et abondant	0	1	0 0,5 0,75 0,85 1	-
Variable	0 0,05 0,10 0,25 0,5	1	0	1

L'initialisation du modèle s'est faite à partir d'une population de base simulée pendant 20 ans dans un environnement constant et abondant avec un taux de réforme fixe afin de garder une taille de troupeau constante et d'atteindre un équilibre démographique. Durant cette période, les individus réformés volontairement ont été choisis au hasard de façon à stabiliser les performances moyennes. Les différentes stratégies ont ensuite été simulées pendant 40 ans et répliquées 20 fois chacune. La réforme volontaire a été appliquée à un taux constant de 25% lors de la sélection et le renouvellement a été déterminé de façon à maintenir la taille totale du troupeau (i.e. le nombre d'individus juste après sélection) constant et égal à 500 femelles et 10 mâles. Les 10 mâles ont été entièrement remplacés chaque année.

Dans cette synthèse nous nous focalisons sur les effets observées à l'issu des 40 années de sélection plutôt que sur le développement de ces effets au cours de la sélection.

Résultats

i. Effets simulés de différentes stratégies de sélection dans un environnement constant : focus sur les effets d'une sélection pour l'efficacité

Sur le long-terme, une sélection uniquement sur la production laitière dans un environnement abondant et constant ne compromet pas la survie des animaux car ceux-ci développent leur capacité d'ingestion au fur et à mesure des générations. Au niveau des caractéristiques héritables de l'allocation de la ressource ce développement se traduit essentiellement par une baisse de la priorité à déposer des réserves corporelles (d_0) ce qui, en raison de la hiérarchie de l'allocation considérée (Figure 9), profite aux autres fonctions (gestation, lactation, croissance, survie). Comme l'allocation pour la lactation (l_0) n'augmente que modérément c'est principalement la croissance et la survie qui bénéficient de la baisse de d_0. Etant donnée la formalisation de l'acquisition dans le modèle, l'augmentation de la taille couplée à la diminution des réserves permet ainsi le développement de la capacité d'ingestion.

Lorsque ce développement est volontairement limité en pénalisant le poids vif dans l'index de sélection (Figure 11), alors la pression de sélection pour la production laitière force une réallocation de l'énergie vers la lactation (l_0 augmente) ce qui compromet le taux de survie dans le troupeau (SURV). Le rapport MILK/BW est ici utilisé pour approximer l'efficacité. Au-delà d'une certaine pénalité ($- W_{BW} > 0{,}85$), sélectionner pour une grande efficacité conduit à l'effet inverse et le taux de survie s'écroule. Lorsqu'une pénalité sur le poids est appliquée alors au cours de la sélection, la diminution de l'allocation d_0 par rapport à sa valeur initiale (0,25) est atténuée. En effet, une valeur faible de d_0 favorise la croissance lorsque les animaux ne sont pas encore matures. Ainsi, l'augmentation de l_0 associée au développement limité de la capacité d'ingestion finit par affecter la survie de façon dramatique, ce qui limite ensuite le progrès de la production laitière dans le troupeau et ainsi l'efficacité.

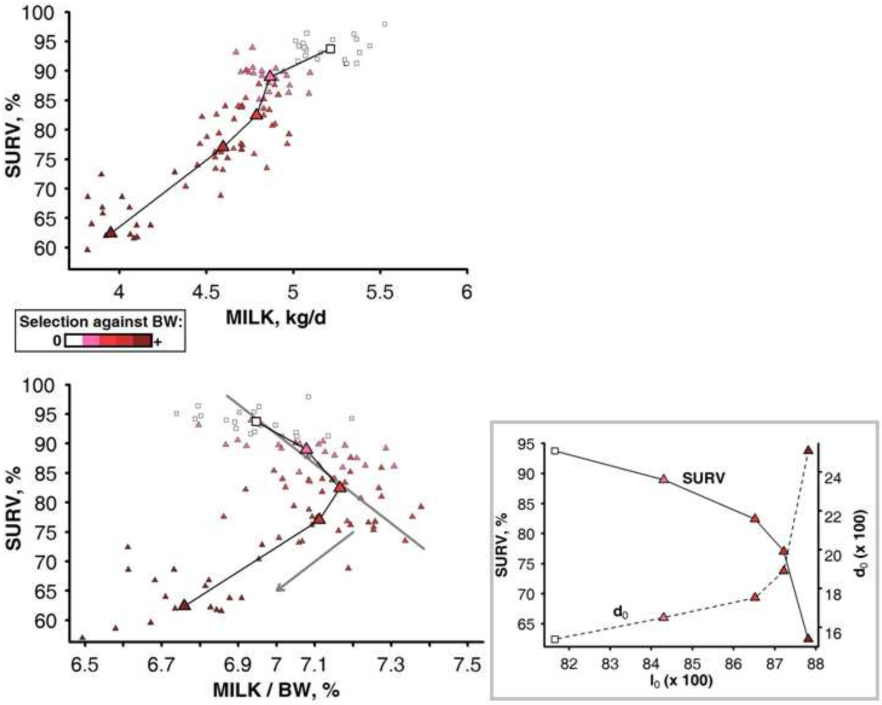

Figure 11 : Relations entre le taux de survie du troupeau (SURV) et la production de lait (MILK) seule (en haut à gauche) ou relativement au poids vif moyen (MILK/BW) (en bas à gauche) après 40 ans de sélection sur la production laitière uniquement (carré blanc) ou en combinaison avec une pénalité sur BW (-0,5 ; -0,75 ; -0,85 ; -1, représentée selon le dégradé) dans un environnement constant et abondant. La moyenne est indiquée (symbole large) avec n=20 réplications (petits symboles). Une pénalité croissante sur BW conduit à une augmentation de la composante héritable de l'allocation vers la lactation (l_0, en bas à droite) par rapport à sa valeur initiale en début de sélection (0,75). Ainsi la survie devient de plus en plus compromise et la diminution de l'allocation vers les réserves (d_0) par rapport à sa valeur initiale en début de sélection (0,25) ne peut se produire ce qui limite le progrès de la production laitière (graphiques de gauche).

ii. Effets observés d'une conduite en lactation longue (LL)

Notre suivi expérimental de la LL a permis de caractériser une reprise de la production laitière environ 50 semaines après la mise-bas (Figure 12). Cette augmentation repose clairement sur un mécanisme différent de celui généralement décrit post-partum. D'une part, les chèvres en LL ont montré une reprise nette non-seulement de la production laitière et de l'ingestion mais aussi du poids. Ainsi nous avons mesuré un bilan énergétique positif en début de LL. D'autre part, la reprise de l'ingestion a semblé être l'élément moteur prédéterminant les dynamiques de performance observées. Ces deux éléments font de la LL un mécanisme particulier car le début de LN est généralement associé à un bilan énergétique négatif et c'est la production laitière qui entraine un changement des autres variables zootechniques.

A partir de cette caractérisation de la LL, deux nouveaux éléments ont été inclus dans le profil temporel de performance du sous-modèle animal: 1) une augmentation transitoire de l'acquisition des ressources déclenchée par un signal saisonnier à environ 330 jours de lactation, et 2) une augmentation de l'allocation des ressources vers les réserves corporelles (d) et vers la lactation (l), se produisant quasi simultanément avec le changement de l'acquisition. Ces éléments ont été paramétrés à partit des données de la LL de notre suivi puis testés dans les scénarios de sélection en environnement variable.

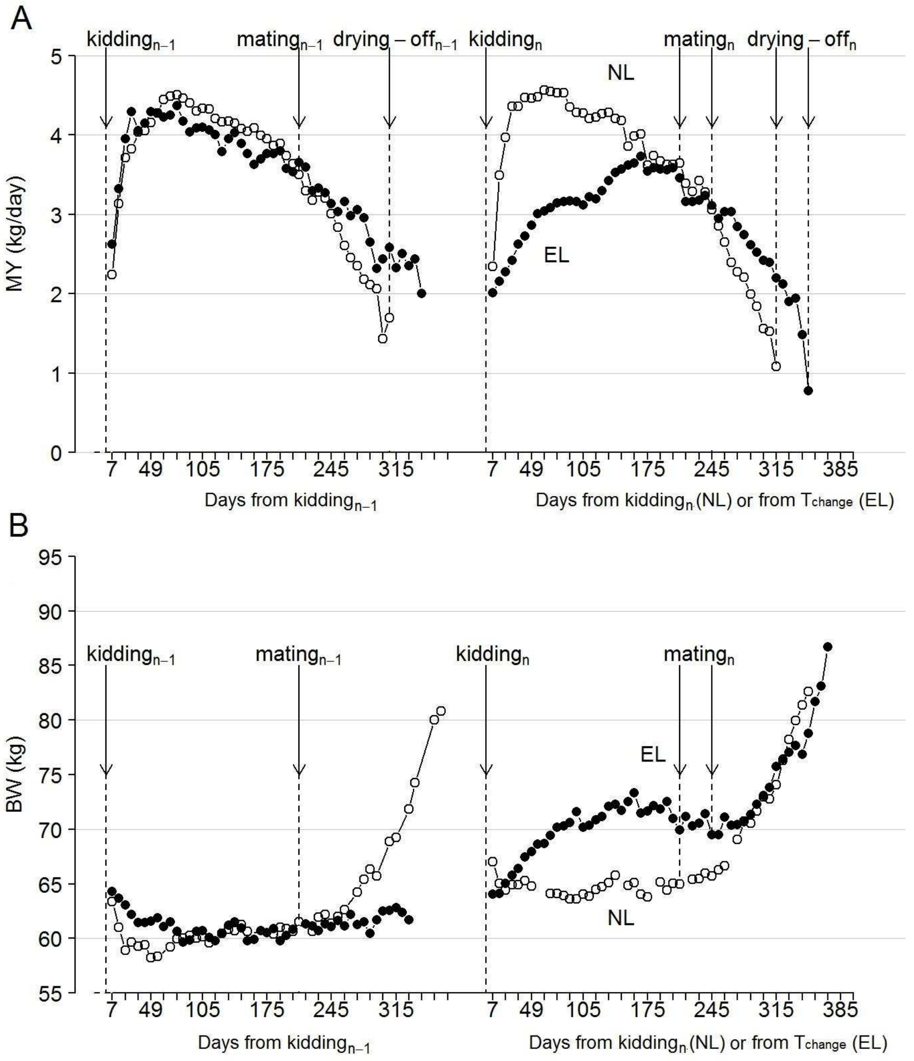

Figure 12 : (A) Variations de la production de lait (MY) et (B) et du poids vif (BW) pour des chèvres en lactation longue (EL ; •, n = 9) et en lactation normale (NL ; ○, n = 9). La période n-1 désigne les phases de lactation « classiques » (pic + baisse) suivant la mise-bas. La période n désigne la lactation associée à la mise-bas suivante chez les chèvres NL et les phases spécifiques observées chez les chèvres en lactation longue. Le point temporel utilisé pour distinguer les deux périodes correspond à une reprise de la lactation chez les chèvres EL.

iii. Effets simulés d'une interaction sélection × LL dans un environnement variable

En environnement variable, nos résultats ont montré une augmentation de la survie lorsque qu'un objectif de sélection pour la longévité ($W_{AGE} > 0$) est combiné à la production (Figure 13).

Par ailleurs, lorsque W_{AGE} est augmenté dans l'index de sélection alors les femelles âgées et hautes productrices deviennent de plus en plus favorisées même si elles ont échoué à la reproduction. Ainsi, au-dessous d'une certaine valeur de W_{AGE} (entre 0,10 et 0,25), un compromis apparait entre MILK et SURV mais au-delà de cette valeur la proportion de LL dans le troupeau (EL) augmente considérablement ce qui conduit à un dépassement du compromis lait-survie. Au niveau de l'allocation, l'augmentation de la proportion de LL modifie la direction des réponses à la sélection. Ceci est lié aux caractéristiques biologiques de la LL observées dans la partie précédente. D'une part, les femelles en LL ne subissent pas de stress métabolique autour de la mise-bas. D'autre part, elles disposent de plus de temps pour reconstituer leurs réserves corporelles pendant la lactation et leur capacité à le faire est accrue. Ainsi, leurs chances de survie et de reproduction sont améliorées pendant la LL. La forte pression de sélection sur d_0 est alors diminuée avec une forte proportion de LL. Cette diminution de d_0 n'est pas compensée par une augmentation de l_0 donc la taille et la capacité d'acquisition augmentent de même que le lait. En revanche, l'efficacité n'est alors pas améliorée.

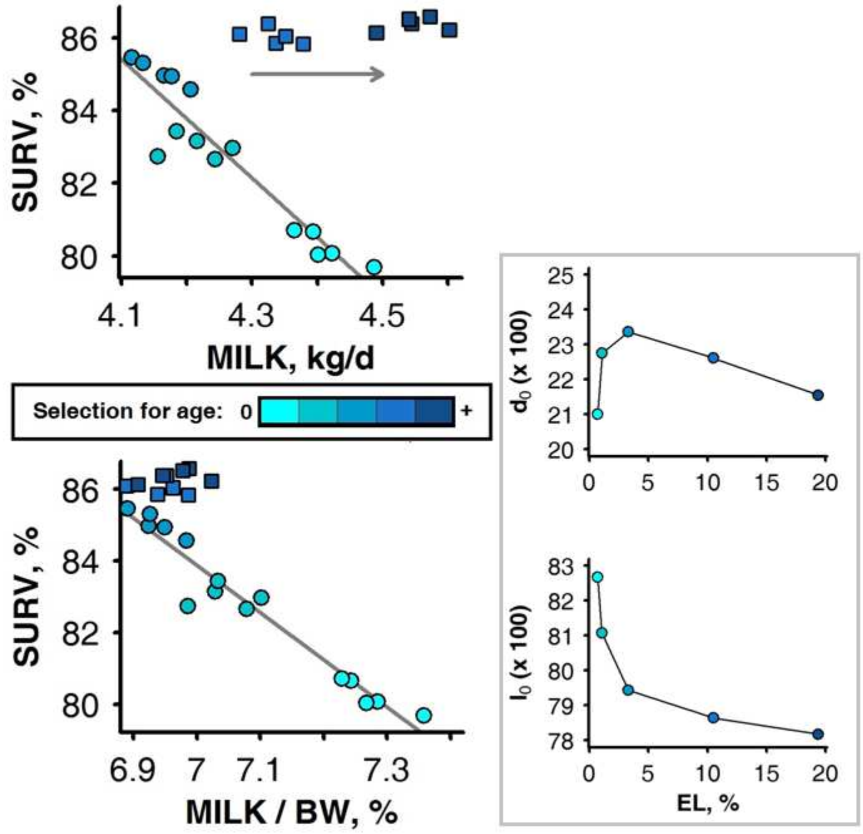

Figure 13 : Relations entre le taux de survie du troupeau (SURV) et la production de lait (MILK) seule (en haut à gauche) ou relativement au poids vif moyen (MILK/BW) (en bas à gauche) après 40 ans de sélection sur la production laitière uniquement (bleu cyan) ou en combinaison avec une sélection sur l'âge (0,05 ; 0,10 ; 0,25 ; 0,5 représentée selon le dégradé) dans un environnement variable. La moyenne des 5 dernières années de simulation est indiquée (n = 20 réplications). Une sélection croissante sur l'âge

conduit à une augmentation de la proportion de lactations longues dans le troupeau (EL en bas à droite). Au delà d'une certaine proportion la priorité à déposer des réserves (d_0) pour augmenter la survie diminue de même que la pression de sélection imposée sur l'allocation vers la lactation (l_0). Ainsi une augmentation de l'acquisition est privilégiée ce qui augmente la production laitière mais pas l'efficacité en raison de l'augmentation de BW (graphiques de gauche).

Discussion

Les résultats des simulations réalisées dans cette thèse mettent en évidence des interactions complexes entre la sélection et la conduite du troupeau lorsqu'elles sont pratiquées dans le même environnement de troupeau. D'une façon générale, des différences locales de l'environnement du troupeau favorisent différentes combinaison de priorités d'allocation de la ressource au fur et à mesure des générations. En retour, l'expression de ces priorités d'allocation détermine la forme des compromis évolutifs entre traits de caractères.

Ainsi, dans un environnement contrôlé et abondant, la sélection d'un haut niveau de production laitière ne dégrade pas la probabilité de survie tant que le développement de la capacité d'ingestion suit la progression génétique de l'allocation de l'énergie ingérée vers le lait. Cette condition est de moins en moins respectée lorsque l'objectif de production est progressivement réorienté vers la recherche d'une efficacité à court terme (i.e. forte production laitière élevée combinée à de faibles coûts d'alimentation) et un compromis entre l'efficacité de la production laitière et la survie émerge alors (Figure 11).

Dans un environnement incontrôlé et variable, nos résultats indiquent que toute augmentation de la production de laitière s'accompagne d'une diminution des chances de survie, à moins que la priorité de l'éleveur sur la régularité de la reproduction ne soit diminuée. Dans ce cas, le compromis production-survie peut-être dépassé en combinant une proportion de lactations longues dans le troupeau avec un objectif de sélection alliant production et longévité (Figure 13).

Dans les deux cas, la sélection dans le troupeau est contrainte par un compromis entre la survie et la production laitière ou l'efficacité de cette production. Au niveau de l'allocation de la ressource, la baisse de la survie s'explique par le mécanisme général mis en évidence dans le modèle de Van Der Waaij (2004), à savoir que la sélection pour un des critères de production exerce la pression la plus forte sur la fonction la plus limitante (dans notre cas l_0) ce qui diminue la quantité allouée à la survie. Par ailleurs, les résultats de cette thèse indiquent qu'un ajustement des priorités de conduite (par exemple, la gestion des échecs à la reproduction) peut changer la direction de sélection et améliorer le compromis. Avant de discuter l'implication de ces résultats sur les contraintes et opportunités d'exploiter les interactions G × E dans le troupeau, nous discutons la portée du principe d'allocation sur le plan biologique. Sur ce plan, l’émergence des compromis évolutifs démontre clairement l'importance des trois principaux mécanismes par lesquels les animaux expriment leurs objectifs évolutifs durant leur vie : 1) leur contrôle d’un niveau désiré de l’ingestion, 2) leur stratégie de préservation de l’espèce s'appuyant sur les réserves corporelles et 3) leur approche tactique pour faire face au coût de reproduction.

Contrôle d’un niveau désiré de l’ingestion. Dans un environnement nutritionnel abondant, la théorie de l’allocation prédit qu’une augmentation de la capacité d'acquisition de la ressource au cours des générations est une condition nécessaire pour augmenter la production de lait sans compromettre la survie (Beilharz et al., 1993, Figure 2B). Avec l’augmentation de l’acquisition, telle qu’elle est formalisée dans le modèle, la sélection pour la production laitière conduit à une réduction systématique de la proportion de réserves corporelles. Ceci s’explique à la fois par un effet de dilution lié à l’augmentation de la taille et par une diminution de la priorité à déposer des réserves. Ces résultats corroborent les évolutions observées en vache laitière hautement sélectionnée sur la production (e.g. Coffey et al., 2004). Toutefois, l’explication fournie par le modèle diffère de l’hypothèse généralement admise selon laquelle la diminution des réserves est la conséquence d’un progrès trop limité de l’ingestion par rapport au progrès génétique du potentiel laitier (Veerkamp et al., 2003; Dillon et al., 2006). Dans le modèle, la diminution des réserves corporelles fait plutôt partie d’une stratégie évolutive favorisée par la sélection et le milieu ; c’est le *moyen* grâce auquel l’acquisition peut-être augmentée. La réussite de cette stratégie dépend de la fourniture d’un environnement peu limitant comme cela peut-être le cas en situation d’élevage laitier intensif (Windig et al., 2005). En pratique une pénalité sur le poids semble finir par être appliquée dans les index de sélection (comme cela a été simulé ici) pour garder la maitrise des coûts de production (Veerkamp, 1998). Dans ce contexte, la mise en évidence d’une limite biologique au progrès de l’ingestion semble compliquée mais essentielle pour valider l’existence possible d’une stratégie évolutive basée sur l’amenuisement des réserves corporelles.

Stratégie de préservation de l’espèce s'appuyant sur les réserves corporelles. Dans un environnement variable, nos simulations montrent qu’une proportion de réserves corporelles est maintenue bien que cela ne soit activement sélectionné par l’éleveur. Par ailleurs, cette proportion s’accroit lorsqu’un critère de longévité est considéré en plus d’un critère de sélection pour la production. Dans l’ensemble ces résultats soulignent le rôle central des réserves corporelles dans la stratégie de préservation des espèces longévives (Sæther, 1997; Gaillard and Yoccoz, 2003; Hamel et al., 2010). Dans les milieux naturels sujets à des variations importantes, ces espèces ont développé au cours de leur évolution naturelle des stratégies qui privilégient la longévité plutôt que la reproduction pour maximiser leur valeur sélective. Leurs traits de caractères liés à la survie semblent avoir été fixés du fait des processus de sélection naturelle ayant agi dans le passé. Le contrôle désiré de l'ingestion et d'un niveau cible de réserves corporelles dans le modèle s'inscrivent parmi ces stratégies (Illius et al., 2002). En effet, dans un environnement limité i) la sélection uniquement pour le lait compromet fortement la survie, ii) lorsque cette sélection est contrebalancée avec un critère de longévité alors la survie est améliorée avec la priorité stratégique à maintenir des réserves corporelles enfin iii) dans un environnement peu limitant cette stratégie évolutive est défavorisée et laisse place à celle décrite dans le paragraphe précédent. En milieux naturels, l'expression des stratégies de préservation des espèces longévives rend difficile la détection des coûts de reproduction sur la survie maternelle (Hamel et al., 2010). De ce point de vue, les situations d'élevage exerçant de fortes pressions de sélection sur la reproduction peuvent rendre ces coûts plus apparents et contribuer à l'étude des compromis évolutifs entre la survie et la reproduction (Mysterud et al., 2002).

Approche tactique pour faire face au coût de reproduction. La relation entre les réserves corporelles et la fertilité représente l'effet secondaire indésirable le plus évident de la sélection pour la production laitière (Rauw et al., 1998) tout comme dans les simulations réalisées en environnement abondant et constant. Dans le modèle, la probabilité de conception dépend directement de la proportion de réserves corporelles et de leur taux de variation. Ce type de contrôle dérive de considérations évolutives (Friggens, 2003; Friggens et al., 2004) et notamment de l'aversion au risque que représente cette tactique en adéquation avec la priorité de survie des mammifères longévives (Bårdsen et al., 2011). L'engagement de la femelle dans un cycle reproductif peut en effet avoir des conséquences négatives pour sa survie future pendant les périodes de forte dépense d'énergie (fin de gestation et début de lactation), en particulier si la femelle ne dispose pas suffisamment de réserves pour faire face à une baisse de la ressource. Si ce contrôle tactique de la reproduction est encodé dans le patrimoine génétique du fait des processus de sélection naturelle ayant agi par le passé, alors il n'est pas si surprenant de constater qu'il s'avère relativement inadapté aux conditions d'un environnement abondant et sécurisé (Stubbs and Tolkamp, 2006).

En milieu naturel, un coût de reproduction est fréquemment détecté entre la reproduction courante (i.e. lactation) sur la reproduction future (i.e. lactation ou conception ultérieure) est (Hamel et al., 2010). Notre caractérisation de la LL suggère également que l'espèce caprine a développé des mécanismes pour compenser une fertilité réduite post-partum au cours de l'évolution (comme la reproduction est aussi une composante majeure de fitness). Ainsi, l'augmentation simultanée observée dans la production de lait et du poids vif pourrait bénéficier à l'allaitement des jeunes et à la probabilité de conception de la mère. Dans un contexte d'élevage, nos résultats de simulation indiquent que la conduite d'une partie du troupeau en lactation longue offre l'opportunité de promouvoir la stratégie de préservation de l'espèce tout en réalisant des gains de production.

Implications pour l'exploitation des interactions G×E dans le troupeau. Dans l'ensemble, nos résultats indiquent qu'un environnement variable augmente les opportunités de valoriser durablement les interactions G × E ainsi que les capacités biologiques des animaux par rapport à environnement constant et abondant. Cette conclusion converge avec les incitations récentes à davantage intégrer des considérations écologiques dans la recherche sur les systèmes d'élevage (Provenza, 2008; Bocquier and Gonza, 2010; Hackmann and Spain, 2010; Dumont et al., 2013a), notamment pour réduire la consommation d'intrants nécessaires à la production.

En situation d'élevage intensif, le contrôle d'un milieu nutritionnel riche et constant impose une maitrise des coûts de production et donc le besoin d'animaux efficaces. Un des moyens d'y parvenir est de sélectionner la production tout en pénalisant le poids vif mature dans les index de sélection (Veerkamp, 1998), de façon à favoriser une allocation directe des nutriments depuis l'aliment ingéré vers le lait produit. Du point de vue du troupeau, cette solution semble compromise à long-terme et pourrait contribuer à l'augmentation des problèmes de santé, à moins que la qualité des rations distribuées ne soit encore améliorée, ce qui semble difficile à réaliser dans le futur (Nardone et al., 2010). Dans ce contexte, les bénéfices d'une augmentation de l'efficacité à court terme pourraient-être insuffisants pour compenser l'augmentation des coûts sanitaires et de remplacement (Benoit et al., 2009). Un nouvel enjeu qui s'impose semble de pouvoir réorienter les objectifs de sélection depuis une efficacité à court-terme vers une efficacité à l'échelle de la vie entière de l'animal dans le troupeau. Face à cet enjeu, certaines combinaisons de sélection et de conduite dans le troupeau représentent des solutions prometteuses. Dans un environnement peu contrôlé, nos résultats indiquent que la priorité de l'animal à maintenir des réserves corporelles est naturellement favorisée et l'inclusion d'un objectif de longévité agit en synergie avec la stratégie évolutive de préservation de l'espèce. Dans un environnement très contrôlé, la conception de stratégies d'alimentation basées sur des variations de la disponibilité pourrait aussi permettre de valoriser efficacement les variations innées des réserves corporelles durant le cycle reproductif (André et al., 2010, 2011).

Dans un environnement variable, nous avons montré une synergie entre une sélection alliant production laitière et longévité et l'utilisation d'une proportion de lactations longues dans le troupeau. Ainsi, les femelles hautes productrices ayant échoué à la reproduction peuvent-être conservées plus longtemps et avec de meilleures chances de survie. Même si leur efficacité est amoindrie pendant leur LL, cela peut-être acceptable dans les systèmes basés sur le pâturage car un haut niveau d'ingestion d'herbe y est économiquement souhaitable (Kolver et al., 2002). Ces résultats convergent avec ceux obtenus dans systèmes bovins-laitiers basés sur le pâturage où les génotypes les plus spécialisés s'avèrent les plus intéressants pour la conduite en lactation longue (Kolver et al., 2007). Cela offre des perspectives intéressantes pour la gestion de la variabilité individuelle dans le troupeau à partir d'effets interactions G × E. Par exemple, une option serait de combiner une proportion de génotypes spécialistes conduits en LL avec une proportion de génotypes plus généralistes capables de se reproduire régulièrement chaque année assurant ainsi le renouvellement dans le troupeau. Le principe de cette option s'applique déjà dans certains troupeaux pastoraux multi-espèces afin de sécuriser le système de production face à évènements climatiques extrêmes (Tichit et al., 2004). Il ne semble pas encore avoir été étudié dans le cas de troupeaux mono-spécifiques où il pourrait représenter une piste pour la conception de systèmes élevage résilients.

Limites du modèle. Le modèle développé dans cette thèse s'est focalisé sur la l'interaction entre les réponses à la sélection et les réponses nutritionnelles dans le troupeau sans représenter très finement chacune de ces réponse. Plusieurs limites en découlent. En ce qui concerne les réponses à la sélection :

- l'index de sélection n'utilise que l'information phénotypique de l'année en cours pour sélectionner les animaux (sauf pour le renouvellement qui est sélectionné sur l'ascendance maternelle). Les informations sur les performances réalisées au cours de la carrière de l'animal, ainsi que celles des autres parents (par exemple, demi-sœurs) pourraient-être utilisées pour estimer plus précisément la valeur génétique des animaux,

- la sélection des géniteurs mâles est faite de façon très élémentaire sans par exemple simuler un testage sur la descendance comme c'est généralement le cas dans les schémas de sélection. Si une partie des gamètes mâles était importée dans le troupeau, notamment grâce à l'insémination artificielle, il conviendrait de représenter ce processus permettant d'accélérer le progrès génétique dans le troupeau,

- l'accouplement a été supposé aléatoire alors qu'en pratique l'éleveur peut le planifier (même si c'est peu le cas en chèvre laitière en monte naturelle) à la fois pour réunir des parents complémentaires et pour gérer la consanguinité.

En ce qui concerne les réponses nutritionnelles :

- notre définition de l'environnement est assez restreinte. Nous n'avons pas représenté d'autres nutriments qu'une énergie métabolisable (e.g. azote). Par ailleurs bien d'autres facteurs environnementaux ont un rôle crucial lors de la sélection (e.g. température, conditions sanitaires) et sont d'ailleurs souvent très contrôlés lors de la sélection des géniteurs élites,

- la formalisation de l'acquisition de la ressource incorpore de façon très simplifiée l'effet d'encombrement de la ration (en considérant une qualité globale) par rapport à la représentation dans les systèmes d'alimentation. Cette formalisation pourrait-être complexifiée surtout si les variations de la qualité des ressources devaient être simulées,

- la conduite du troupeau n'est pas ajustée au cours de simulations (occurrence des évènements de reproduction et de réforme invariable, taille du troupeau constante d'année en année). D'autres ajustements de conduite que la LL permettent de gérer les échecs à la reproduction (e.g. plusieurs épisodes de reproduction dans l'année) et pourraient également révéler des opportunités d'améliorer le compromis lait-survie mis en évidence. Sur le plan biologique, cela nécessiterait de prendre en compte la saisonnalité de la reproduction essentielle chez les petits ruminants.

Evaluation. En plus des limites des modèles évoquées ci-dessus, une évaluation approfondie du modèle serait souhaitable. Cette évaluation semble compliquée à aborder en raison des différents niveaux de paramètres à tester, à savoir 1) les paramètres génétiques des traits héritables (ici ceux utilisés pour déterminer l_0 et d_0) qui influent directement sur les réponses à la sélection, 2) les paramètres des probabilité de survie et de conception qui influent sur la démographie du troupeau indépendamment du contrôle de l'éleveur, et 3) les paramètres d'acquisition et d'allocation de la ressource dans le sous-modèle animal.

Par ailleurs, toute analyse de sensibilité de ces paramètres et leur interaction sera dépendante de la structure hiérarchique d'allocation de la ressource que nous avons choisie (Figure 9). En effet, la variation de l'allocation considérée à un niveau donné de la hiérarchie affecte la variation dans les niveaux suivants, ce qui influe sur la direction et la vitesse de la réponse à la sélection. Worley et al. (2003) ont ainsi mis en évidence ces effets complexes à partir d'un modèle hiérarchique simple (soit deux niveaux hiérarchiques de l'allocation avec un pas de temps d'une génération et sans interdépendance entre l'acquisition et l'allocation). S'attaquer à l'évaluation approfondie de notre modèle semble donc un projet compliqué mais qui devrait néanmoins être abordé. Au stade actuel, le comportement du modèle sous différents scénarios de simulation (sélection et la variation de l'environnement) s'accorde suffisamment avec les phénomènes observés dans la littérature pour suggérer une certaine validité générale.

Perspectives

Deux principales perspectives se détachent de cette thèse. La première serait de pouvoir mieux évaluer la validité et la portée de notre description génétique de l'animal en se rapprochant davantage de données observées. La seconde serait d'intégrer davantage la composante décisionnelle du système d'élevage dans le modèle. La complémentarité de ces deux perspectives pourrait permettre de faire évoluer le modèle vers un outil à partir duquel aborder la conception de systèmes résilients.

Description génétique de l'animal. Pour augmenter la valeur prédictive du modèle et le tester, il conviendrait de pouvoir estimer ses composantes génétiques. Pour ce faire, l'approche standard en génétique quantitative est de partir des traits de caractères observés (phénotype) puis de combiner une large quantité d'informations avec l'utilisation de techniques de régression pour dissocier les effets génétiques de ceux de l'environnement (Figure 14, haut). Dans une approche mécaniste, le point de départ est une description génétique de l'animal (à partir de caractéristiques indépendantes de l'environnement) qui sert ensuite à simuler la réponse phénotypique à des conditions de l'environnement spécifiées en entrée du modèle (Figure 14, bas). Les caractéristiques utilisées pour décrire le génotype sont supposés être étroitement liées à la biologie de l'animal (et donc à ses gènes), et donc être stables à travers différents environnements (Doeschl-Wilson et al., 2006). A l'inverse, dans l'approche standard utilisée en génétique quantitative l'estimation de ces caractéristiques est dépendante du jeu de données et notamment de l'environnement dans lequel les traits de caractères sont observés. Potentiellement, une approche mécaniste permet de fournir une description générique du génotype, ce qui semble particulièrement intéressant pour accommoder la diversité des environnements de troupeaux rencontrés (Bourdon, 1998). Cela implique de pouvoir estimer les caractéristiques génétiques utilisées ce qui peu ce faire au moyen notamment de techniques d'inversion de modèle (Doeschl-Wilson et al., 2006). Ces techniques ont été appliquées avec succès avec un modèle de croissance chez le porc et à partir d'une description du génotype qui s'apparente à celle généralement considérée dans les modèles nutritionnels (i.e. un potentiel génétique pour le niveau de performance) (Knap et al., 2003; Doeschl-Wilson et al., 2007). Ainsi, une voie privilégiée existe pour mieux tester la portée de notre description génétique ou comme bien celle utilisée dans les nombreux modèles nutritionnels développés en sciences animales.

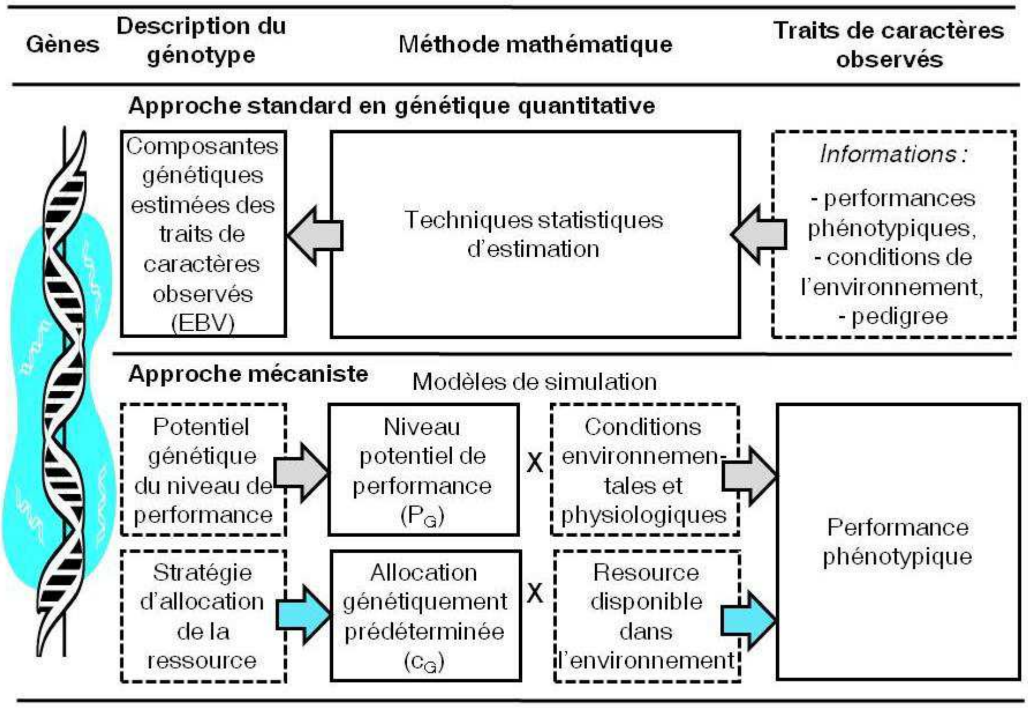

Figure 14 : Représentation des différentes approches du lien entre génotype et phénotype et place de l'approche proposée dans la thèse. Les données d'entrées et de sortie des différentes approches sont encadrées respectivement par des lignes en tirets et continues. Adapté de Doeschl-Wilson et al. (2006)

Représentation de la composante décisionnelle. Du point de vue de l'amélioration génétique à l'échelle régionale ou nationale, des descripteurs synthétiques de l'environnement du troupeau facilitent la prise en compte de cet aspect dans les méthodes statistiques d'estimation (Calus et al., 2005). Du point de vue du système d'élevage, ces descripteurs peuvent masquer des variations importantes de conduite liées non seulement à l'environnement global du système (e.g. situation géographique, orientation technico-économique de l'exploitation) mais aussi aux priorités stratégiques des éleveurs. Ces priorités contrastées jouent un rôle déterminant dans la gestion des réformes (Beaudeau et al., 1996; Ahlman et al., 2011) ce qui peut laisse penser qu'elles déterminent aussi les décisions stratégiques de sélection. Dans cette thèse, les interactions G × E sont représentées comme le résultat d'un processus dynamique multi niveaux impliquant l'éleveur, plutôt qu'un terme statistique. Au stade actuel, ce processus intègre de façon très sommaire l'influence de la conduite d'élevage. Pour mieux intégrer cet aspect, il conviendrait de représenter la façon dont l'éleveur influence et ajuste continuellement la conduite et la sélection en fonction du contexte de production (e.g. du prix du lait et des aliments) et des performances du troupeau (e.g. volume de lait réalisé). L'articulation des dynamiques décisionnelles et des dynamiques biologiques représente un défi conceptuel majeur pour identifier les propriétés émergentes du système d'élevage et concevoir des modes de conduite résilients. L'étude de l'évolution des priorités de l'animal lors de la sélection constitue seulement un premier pas vers cet objectif car c'est la coévolution de ces priorités avec celles de l'éleveur qui permettra de quantifier le risque d'inadéquation entre les génotypes et l'environnement du troupeau.

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Selecting those animals that have the greatest level of production, with little regard for other traits, has historically worked well in a favorable environment (i.e. nutrient-rich diet, low pathogen load, thermoneutrality). However, for numerous reasons (economic, climatic, ecological) farmers will find it increasingly difficult, and indeed may actively choose not, to provide such favorable conditions in their herd environment. Selecting animals that match the future herd environments thus becomes as important as managing the herd environment to match the selected genotypes. To better identify constraints and opportunities to apply these two options, we propose, for the first time, in this thesis an animal model integrating the effects of selection and management. This model integrates resource allocation between life-functions resource as heritable traits. It enables simulating short-term performance and long-term selection response resulting from the transmission of allocation traits between generations. The model was applied to the dairy goat and focused on the management of extended lactation (EL) for a part of the herd (management practice based on keeping females in lactation without a new reproductive cycle). Both selection and management were assumed to influence the way every animal allocates its resource between functions. We aimed to assess the significance of this assumption for a better understanding of the development of genotype-environment interactions (G × E) over the long-term. In a herd subject to variations in the feeding level, different selection strategies aiming at improving milk production and longevity were simulated. In agreement with the resource allocation theory, the selection responses show improving production and survival has to face a trade-off between these two traits. However, this trade-off is alleviated when selection is combined with some proportion of EL in the herd. Such a synergistic effect between selection and management results from a complex interaction between the individual dynamic performance during EL and the herd turnover. Thereby, the innate capacity of goats to extend their lactation might be promoted to enhance herd resilience.

Key words: resource allocation, herd environment, genotype-by-environment interactions, modeling, simulation, extended lactation, dairy goat

Sélectionner les animaux qui ont le plus haut niveau de production, en tenant peu compte d'autres caractères, a toujours bien fonctionné dans les conditions d'un environnement favorable (i.e. ration riche en nutriments, faible charge pathogène, thermoneutralité). Toutefois, pour de nombreuses raisons (économiques, climatiques, écologiques), les éleveurs auront sans doute de plus en plus de mal à réunir de telles conditions dans l'environnement de leur troupeau, et pourront même délibérément choisir de ne pas le faire. Sélectionner des animaux qui soient adaptés avec les conditions futures des troupeaux devient donc tout aussi important qu'adapter la conduite du troupeau en fonction des génotypes sélectionnés. Pour mieux identifier les contraintes et les opportunités d'appliquer ces deux options, nous proposons, pour la première fois dans cette thèse, un modèle animal intégrant les effets de la sélection génétique et de la conduite du troupeau. Ce modèle intègre des coefficients d'allocation de la ressource alimentaire entre les fonctions biologiques en tant que caractères héritables Il permet de simuler à court-terme les performances zootechniques et à long-terme les réponses à la sélection résultant de la transmission de ces caractères d'allocation entre générations. Le modèle a été appliqué à la chèvre laitière et se focalise sur la conduite en lactation longue (LL) d'une partie des chèvres du troupeau (conduite consistant à préserver des femelles en lactation ayant après une mise bas sans réengagement d'une nouvelle reproduction). Nous sommes partis du principe que la sélection et la conduite du troupeau influencent tous deux la façon dont chaque animal alloue ses ressources entre ses fonctions biologiques. Nous avons cherché à évaluer la portée de ce principe pour mieux comprendre le développement des interactions génotype-environnement (G × E) sur le long terme. Dans un troupeau soumis à des variations du niveau d'alimentation, différentes stratégies de sélection ciblant l'amélioration de la production laitière et de la longévité ont été simulées. En accord avec la théorie de l'allocation, les réponses à la sélection révèlent que l'amélioration de la production et de la survie doit faire face à un compromis entre ces deux caractères. Cependant, ce compromis est atténué lorsque la sélection est combinée avec la conduite en LL d'une partie du troupeau. Un tel effet de synergie entre sélection et conduite résulte d'une interaction complexe entre la dynamique individuelle de performance au cours de la LL et le renouvellement du troupeau. Ainsi, la capacité innée des chèvres à prolonger leur lactation semble pouvoir être valorisée pour améliorer la résilience du troupeau.

Mots clés : allocation de la ressource, environnement du troupeau, interactions génotype-environnement, modélisation, simulation, lactation longue, chèvre laitière