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How models contribute to livestock farming system research: Overview of recent advances

M. Tichit^{*, **}, L. Puillet^{*, **, ***} and D. Sauvant^{****, ****}

^{*}INRA, UMR 1048 SAD-APT, F-75231 Paris (France)

^{**}AgroParisTech, UMR 1048 SAD-APT, F-75231 Paris (France)

^{***}INRA UMR 791 PNA, F- 75231 Paris (France)

^{****}AgroParisTech UMR 791 PNA, F-75231 Paris (France)

Abstract. The objective of this paper is to bring insights into the contribution and advance of modelling for livestock farming systems (LFS). First, we rely on a few examples to illustrate how models can be powerful tools to increase our understanding of livestock production. Second, we argue that: (i) the choice of model type depends on the goal that modeller wants to achieve; (ii) any model is a compromise among generality, precision or realism; and (iii) any model requires hypotheses, data and careful evaluation against reality. Third, we develop two examples showing that new challenges faced by LFS demand to incorporate new scales of analysis. The dairy goat model shows that it is possible to simply formalize basic biological processes at female level. This representation is crucial to increase our understanding on the role of the variability of female's lifetime performance at herd level. The co-viability model shows that accounting for grazing impact on the conservation of biodiversity requires enlarging spatial and temporal scale of LFS analysis. It thus implies a simplification of grazing process formalization. Both examples open new fields of collaborations between animal production sciences and other disciplines such as animal nutrition and population ecology.

Keywords. Modelling – Livestock farming system – Ruminant.

Contribution de la modélisation à la recherche sur les systèmes d'élevage : vue d'ensemble des progrès récents

Résumé. L'objectif de cet article est d'illustrer les apports et les progrès de la modélisation des systèmes d'élevage. A partir de quelques exemples, la première partie montre que les modèles sont de puissants outils pour améliorer notre compréhension des systèmes d'élevage. Dans la seconde partie, nous montrons que : (i) le choix du modèle dépend des objectifs poursuivis par le modélisateur; (ii) tout modèle est un compromis entre précision, généralité et réalisme; et (iii) tout modèle nécessite des hypothèses, des données et une phase de validation. Dans la troisième partie, nous développons deux exemples montrant que les nouveaux enjeux auxquels sont confrontés les systèmes d'élevage, impliquent des changements d'échelle pour leur formalisation. Le modèle de chèvre laitière montre qu'il est possible de formaliser simplement des processus biologiques à l'échelle individuelle. Ceci est crucial pour accroître notre compréhension du rôle de la variabilité des carrières au niveau du troupeau. Le modèle de co-viabilité montre que la prise en compte des effets du pâturage sur la biodiversité nécessite d'élargir les échelles spatiales et temporelles pour la modélisation des systèmes d'élevage. Ceci implique donc une simplification dans la représentation du pâturage. Ces deux exemples ouvrent de nouvelles pistes de collaboration entre la zootechnie et d'autres disciplines abordant les systèmes d'élevage telles que la nutrition animale et l'écologie des populations.

Mots-clés. Modélisation – Systèmes d'élevage – Ruminant.

I – Introduction

Modelling livestock farming systems (LFS) is not a new concern as it has been already pointed out by Dent *et al.* (1996). However, since this time, this area of research has progressed and is facing new challenges. The last decade has been a period of radical changes: crisis in consumer confidence in their products, expectations for environmental functions and developments in European and national regulations which generate uncertainties (Tichit *et al.*,

2008). The uncertainty in LFS is, in itself, nothing new (Hardaker *et al.*, 1997) but the multiplicity of the parameters concerned, their interactions and the rate with which they change are increasingly impacting the choices that farmers must make in terms of management. Due to the multiplicity of expected performances, analysis of LFS is becoming more and more difficult. For instance, within a context of rapidly increasing feeding costs (e.g. cereal markets) and uncertainty on output prices (e.g. milk and meat products) the development of feeding systems based on grazed grasslands is a way to secure and increase the global efficiency of LFS. However, as grass resources are highly variable throughout time, the efficiency of LFS will largely depend on the potential of females to adapt and produce in this fluctuating environment (Blanc *et al.*, 2007). Therefore, studying such systems will demand to take animal flexibility into account. Farmers are also increasingly requested to adapt their grassland management, in order to generate suitable levels of habitat quality for the conservation of biodiversity (Hadjigeorgiou *et al.*, 2005). In this context, models can be useful tools to increase our understanding of the properties of such complex systems and to find out new management practices aimed at improving multiple performances.

The objective of this paper is to bring insights into the use of models in LFS research. First, we will rely on a few examples to illustrate what models are and how they can be powerful tools to increase our understanding of livestock production. Secondly, we will show importance of model objectives and the link with the choice of their structure. Thirdly, we will develop two examples showing that emerging challenges in LFS demand to incorporate new scales, either lower or upper, and open new fields of collaborations between animal production sciences and other disciplines e.g. animal nutrition and population ecology.

II – Why do we need models for livestock farming system understanding?

Models are of great interest for analysing LFS which are by nature complex systems. Models make it possible to explore complex systems that cannot be directly manipulated through controlled trials. They also make it possible the study of system behaviour over large extended time steps which are almost impossible with classical experimental devices. Furthermore, models can assist in testing hypothesis and explore numerous contexts of predictions.

Complexity of LFS requires focusing on the relationships among constitutive elements (Systemic approach) rather than on the elements themselves (Cartesian approach). LFS are classically represented as a decision sub-system interacting with a biotechnical sub-system (Gibon *et al.*, 1999). The biotechnical sub-system describes how the different biological functions of animals and resources are modulated by management practices to realise the production process. The decision sub-system represents a frame of rules allowing decisions involved in management process to achieve targets in long (strategy) and short (tactics) terms. Management practices are the links between both sub-systems. On one side, they are the result of decision sub-system and on the other side they become a driver into the biotechnical sub-system. Thus, management practices correspond to two information flows. The first one represents the drivers of farmer's decisions, the second one corresponds to information on the production process which inform farmer in order to adapt management. Animal performances from the biotechnical sub-system generate information which feed back into the decision sub-system in order to adapt management. This feedback leads to an interactive process and makes it possible to capture the dynamic behaviour of LFS. This aspect is central to model their performances because, in these systems, production is not homogeneous over time and is influenced by age (or parity level instead, status...) of reproducing females (Pià, 2007).

As any biological system, biotechnical systems have a hierarchical structure characterised by strong interdependency among organization levels. A given level n gives sense and is dependant upon what happens at lower level $n-1$ and the next higher level $n+1$ incorporates the constraints which impinge on level n , etc. On descending to lower levels, both the spatial and

temporal scales become smaller, thus corresponding to smaller size and faster processes and shorter terms of decision. For instance, the herd (level $n+1$) can be seen as a set of animal groups (level n) each of them being composed of individuals (level $n-1$) (Fig. 1). Each level has its specific descriptors belonging to that level alone. For instance, each female can be described by its own lifetime performance. Each animal group can be described by a certain level of variability in terms of animal performance. This variability emerges from the lower levels, notably the individual responses. Finally, the herd level can be characterised in terms of level and timing of production, age structure, etc. These indicators are irrelevant at lower levels but result from processes at these levels. By this way, the herd level gives rise to emergent properties which do not exist at lower levels.

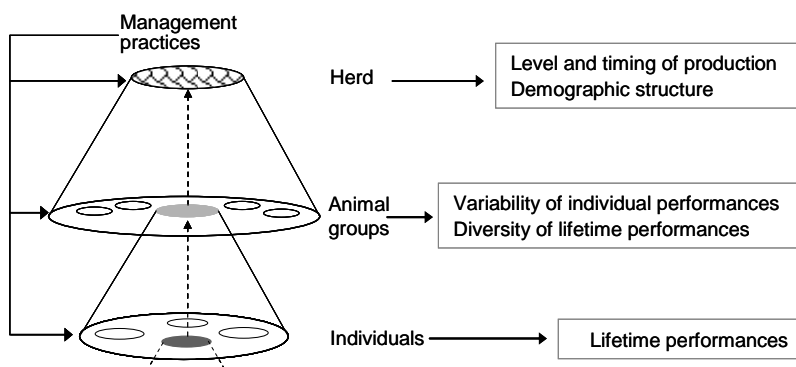


Fig. 1. The herd as a complex and hierarchical system.

Because of LFS complexity and multiplicity of their performances, their evaluation cannot be performed through summarizing. For that, it requires consideration of different and complementary viewpoints as proposed by Landais and Bonnemaire (1996). This viewpoint concept is important because it influences how a given LFS will be modelled according to the type of questions asked by the modeller. At least three major complementary viewpoints summarize the diversity of LFS performances and the specific questions addressed to these systems. The ecological viewpoint makes it possible to assess the environmental performance of LFS. It implies to pay special attention to spatial processes generated at several interdependent scales from fields to landscape. It also requires examining the long term consequences of management on ecological components of ecosystems. The economic viewpoint allows assessing the economic performance of LFS (product quality and price, production costs...). It demands to focus on the insertion of livestock farms into food chains and on technological processes involved in animal product transformation (Lossouarn, 1994). Finally the zootechnical viewpoint leads to focus on animal performances at the different scales involved in herd management and demands to represent biotechnical processes. Each viewpoint demands to integrate knowledge from animal production science (nutrition, genetic, reproduction...) with other disciplines (e.g. ecology or agricultural economics).

III – Ultimate goals of models and choices about their structure

Several model categorizations have been proposed to classify the existing diversity in terms of model types. It is classically considered that model can be empirical or mechanistic, deterministic or stochastic, static or dynamic. Inspired by Monod (1970), Thornley and France (2007) proposed to distinguish another sub-category, referred to as teleonomic, which relates to any of the previous categories and corresponds to goal seeking models. This reference to the teleonomic project of Monod was already applied in animal nutrition (Sauvant, 1996a). Our

purpose is not however to review all model types as several reviews are already available for different fields of animal sciences (e.g. see for instance Sauvant, 1996b, Tedeschi *et al.*, 2005 in animal nutrition; Plà, 2007, Kristensen *et al.*, 2007 in herd management science). Model can also be classified according to their ultimate goal: advisory and application purpose versus research models. Both types do not have the same demand in terms of accuracy and mechanisticity, the first one being the type that may be more demanding in precision. Beyond these aspects, due to the complexity of biological systems, any scientist involved in a modelling project has to choose between building models which trade-off generality, precision or realism (Levins, 1966). According to Levins "there is no single, best purpose all-purpose model", it is possible to continuously improve generality, realism and precision, but essentially in a pair wise fashion. This leads to three model building strategies: in Type I models, generality is sacrificed for precision and realism; Type II correspond to models where realism is sacrificed for generality and precision whereas Type III are models where precision is sacrificed for generality and realism. Indeed, this pair wise fashion is only partially achieved in many modelling situation and consequently models are mainly focused on one component.

To highlight this delicate compromise, we will rely on simple examples related to food intake and we will show that model ultimate goal strongly influences the type of model which is developed. As food intake is a key input for the animal production process of feed/product conversion, many models have been developed to investigate how different animal and environmental factors may predict the observed variability of food intake. Some aim at generating accurate prediction and in this case an empirical model providing a direct link between environmental factors and food intake can be sufficient. At the opposite, others aim at increasing understanding of the complex mechanisms regulating food intake. As underlined by Yearsley *et al.* (2001), neither type are superior, they are just dealing with different questions.

For instance, in their review on intake models for grazing dairy cows, Delagarde and O'Donovan (2005) present a selection of seven static empirical models predicting herbage intake at pasture. These describe a curvilinear increase of intake with available herbage. All models predict a fairly similar daily intake when herbage availability is around 35-40 kg DM cow/d. However on both extremes of the gradient of herbage availability, discrepancies among model predictions are fairly important. Thus, at the lowest levels of grass availability, intake prediction varies from 6 to 15 kg DM cow/d and at the highest levels it varies from 16 to 22 kg DM cow/d. These differences are likely to be related to the range and number of situations under study. This variability in predictions is also an outcome of the research effort which follows the most frequent situations, the lower variability in prediction being obtained on the levels of herbage availability where the more data were available to derive more accurate prediction.

Understanding mechanism involved in food regulation requires a more complicated model structure, representing dynamic processes at two levels at least. They are much more demanding in terms of variables, parameters, determining factors and response laws. They allows for an increase in generality and understanding that may make acceptable the reduction in quantitative accuracy (Yearsley *et al.*, 2001). For instance, the sheep model developed by Sauvant *et al.* (1996c) proposes a fairly simple mechanistic model of intake, chewing activities, and digestion of sheep that integrate aspects of both physical and chemostatic regulation. It combines two interactive sub-models: a rumen digestion model and a feeding and behaviour decision model. The first one describes the major digestive processes and flows of nutrients and provides information on its status to the decision model. The decision model manage the trade-off among three substitutive behaviours: eating, ruminating, and other nonchewing activities (resting, etc.) and simulates estimates of eating durations, rumination and dry matter intake. The model could be parameterised to mirror fairly accurately the major dynamic events related to intake regulation, chewing activities, rumen digestion, and particle movements. Its overall behaviour was checked on its main dynamic features, the kinetics of intake, feeding pattern, and ruminal particles (see below). In comparison to the above examples, this model pursues a research goal and proposes a framework for a more comprehensive view of the individual variations of feeding behaviour. Despite this initial target, based on a sheep at

maintenance and living in a cage, Baumont *et al.* (2004) have incorporated this model, without any simplification in a mechanistic model of sheep intake and grazing behaviour at pasture. Results obtained demonstrated that, if computer capacity is not limiting, a fairly complicated model of animal can be included into a much larger model of animal foraging. However, in many situations changing scale usually requires processes simplifications.

Several types of strategies can be implemented to evaluate models. A first strategy, denoted internal validation, can be process through sensitivity analysis. Alteration of each of the main parameters by a certain % of their standard value makes it possible to identify what parameters are more influential. In the Sauvant *et al.* (1996c) model, sensitivity analysis (variation of 20% of the standard value of each parameter) showed that the most sensitive parameter was the cell wall (NDF) content of the forage. Sensitivity analysis is essential to study the overall model behaviour and to detect parameters values likely to induce unexpected and non realistic behaviour. It is also useful for identifying parameters requiring more accurate measurements. Other aspects, such as determining the singular points and attractors of a model, are often included into the internal validation. A second validation strategy concerns external validation which refers to model ability to accurately predict results for some particular experimental or practical situation. Statistical procedures are available to objective this process. An important principle for external validation is to have an independent data set i.e. that was not used for model parameter calibration. For instance, the simulated eating patterns from Sauvant *et al.* (1996c) model were compared to experimentally measured eating patterns. It showed that simulated eating pattern shapes were roughly in agreement with measured ones with three different feeds (mixed grass, orchard grass and lucerne hay). Validation of stochastic models (i.e. incorporating one or several random parameters) is difficult because predictions have a distribution. One possibility consists in generating a large number of simulation replications and calculating an envelope curve around prediction that defines the possible range of results (Cournut, 2001). A third validation strategy is the expert validation. It consists in simply confronting results with expert knowledge in order to elaborate a critical assessment of the results (see further Figs 2 and 3). One side it is the less desirable one, other side it can be the only possible way especially for complex dynamic simulators where data availability is the main constraint.

Data management around model building and validation is crucial to any modelling project. For both parameters estimation and validation meta-analysis can play an important role at both stages because they offer an efficient way to quantitatively synthesize data from literature. Sauvant and Martin (2006) have proposed to use them as a complementary tool of mechanistic modelling in order to determine the most probable values of constants as well as initial values for state variables (e.g. compartment size). Moreover they can be of particular interest to determine shape, choose the most relevant equations and identify the most probable values of parameters (i.e. fractional rate) linking compartment outflows with the size of donor compartment. They can also be used to generate data synthesis for validation process. Finally, in any modelling project data availability strongly determines the whole validation process. Parameters can have a possible, plausible, observed or studied range and the latter obviously translates the research effort that may cover a limited range of observed values.

IV – New challenges in modelling performances of livestock farming systems

As underlined by Gibon *et al.* (1999), a key issue for LFS sustainability is the appraisal of the lifetime biological operation of reproductive females, in order to understand the consequence of management rules at any stage in their lifetime with respect to herd performance. To our viewpoint, this creates a new challenge for herd simulators which require incorporating some basic biological processes emerging at female level (down scaling). Secondly, environmental issues, notably biodiversity stakes, are inviting animal production scientists to assess more carefully the grazing impact on the conservation of wild plant and animal species. In this case,

livestock production impacts at large temporal and spatial scales need to be accounted for (up scaling). Upscaling is also important for other environmental issues relevant for intensive livestock systems (e.g. management of animal waste see Aubry *et al.*, 2006). Hereafter, we will illustrate these down and upscaling processes that are necessary to derive models able to enrich our understanding of new issues faced by LFS.

1. Down scaling to incorporate driving forces such as biological regulations at the level of individual females

As emphasized by Blanc *et al.* (2007), the ability of livestock farming systems to adapt to a varying environment depends upon the potential adaptability of females. This put in evidence the adaptability of the animal regulations. Homeorhetic regulations (HR) coordinate change in the metabolism of tissues necessary to support the various physiological changes of female organisms (Bauman and Currie, 1980). These regulations are thus determining factors in the organisation of the successive sequences of physiological changes throughout female's productive life. They closely coordinate functions (especially nutrition and reproduction) by changing rules in nutrient partitioning and as a result relative priorities among physiological functions; in contrast they do not adapt to environmental alterations. Beside the HR, homeostatic regulations (HS) constitute a dynamic buffer of environmental variations around trajectories basically calibrated by HR. Thus HS play a key role in organism adaptability and responses to surrounding factors.

Different approaches have been used to formalize these regulations (see Sauvant 1996b for a review of lactating ruminant models). On one side researchers have represented changes in nutrient partitioning through changes in theoretical hormones which control the major flows involved in metabolism. These highly detailed models ignore the successive gestation-lactation cycles and remain at the scale of a single lactation (Baldwin, 1987; Danfaer, 1990, Martin and Sauvant, 2007). However they are more focused on HR regulations. On the other side, herd models (Blackburn and Cartwright, 1987; Sorensen *et al.*, 1992; Tess and Kolstad, 2000) have integrated a minimum of controls of nutrient partitioning over a succession of production cycles. These models still remain inexplicit as to the drivers of these changes. Consequently, they shed no light on the potential adaptability of lactating females as a key for livestock system sustainability in fluctuating environment.

More recently, Puillet *et al.* (2008) developed a dynamic model of a lactating goat, through several lactation cycles, which includes HR through the driving effect of theoretical hormones on the evolution of nutrient partitioning. The model, described below, combines a minimum of mechanistic representations used in models of lactating female with the long term approach developed in herd models. Following the approach proposed by Sauvant (1992), the female organism is represented by two interactive sub-models: the operating sub-system and the regulating one. Operating sub-system represents the productive functions of the lactating female considered as a simple converter of feed into milk. Regulating sub-system stands for HR using theoretical hormones. It directly controls the major physiological flows of the operating sub-system. In order to expand the animal model over the productive history of the female, the model incorporates a third sub-system, the reproductive events sub-system, which coordinates the regulating sub-system through discrete reproductive events corresponding to service, kidding and drying off in order to simulate the whole productive life of a dairy goat.

The model simulates the changes in milk production, dry matter intake and body weight throughout the productive life of a lactating female. The methodological approach was tested by running simulations during five breeding cycles of an average goat (4 kg at birth, 60 kg at maturity and with a production potential of 4.8 kg). The simulated dry matter intake follows changes in milk production with a time delay. The similar trends between milk yield and dry matter intake traduces the fact that in this model intake is determined by milk production (expression of production potential without any feed limitation or excess). The delay between

both peaks traduces the mobilisation of body reserves at the beginning of lactation: the energy from intake does not increase as quickly as the energy exported in milk and body reserves temporarily ensure the energy supply.

Sensitivity analysis were performed to assess how the production potential (POT) parameter contributes to model output variability in terms of milk production (Fig. 2) and body reserves (Fig. 3). The model was run repeatedly for combination of POT values varying from 2 to 6 kg at peak. The maximum value reached at the fourth lactation corresponded to POT. The loss of body reserves during lactation became higher as POT rose. The model assumes that females producing more are also those whose body reserves are most mobilised (Bauman *et al.*, 1985, Morand-Fehr and Sauvant, 1988). This general pattern suggests that the model fairly well simulates the link between a female's ability to produce and mobilise reserves. Globally, these first outputs can be seen as an expert validation showing that general patterns of variables are well represented in the goat model.

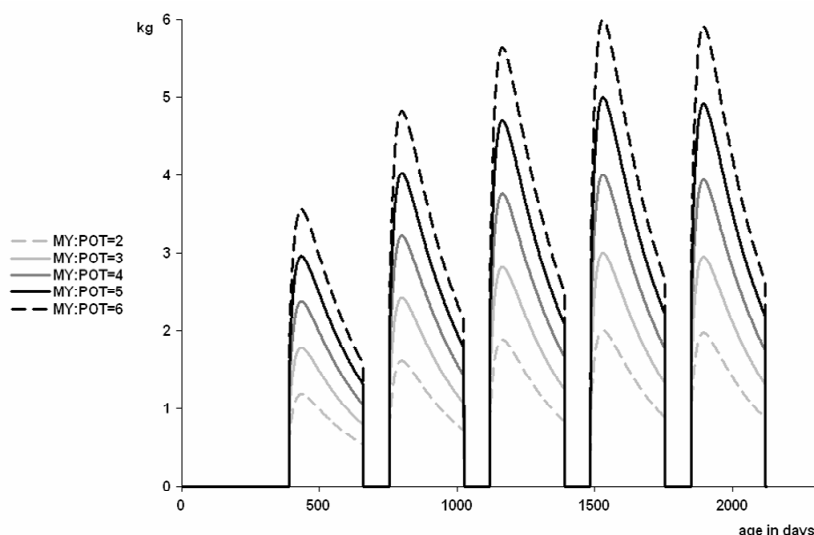


Fig. 2. Simulated kinetics in kg/day of milk yield (MY) of a goat weighing 4 kg at birth, reaching 60 kg at maturity and with a production potential (POT) varying from 2 kg to 6 kg (modified from Puillet *et al.*, 2008).

In a following stage, model outputs for milk yield were validated through thousands of data of milk French control (Puillet *et al.*, 2008). For the other key parameters no comparable large and diverse data set was available, it was thus necessary to evaluate the model through various experimental contexts. Kinetics of DMI was evaluated with data obtained from an INRA experimental flock (Fig. 4). For body weight kinetics, another data set from the same herd was used. Figures 5 and 6 show that simulated reconstitution of body reserves at the end of lactation is too fast whereas simulated persistency of milk production is too low. These observed biases are consistent: as a greater part of energy is driven through reconstitution, a lesser part is driven through milk yield.

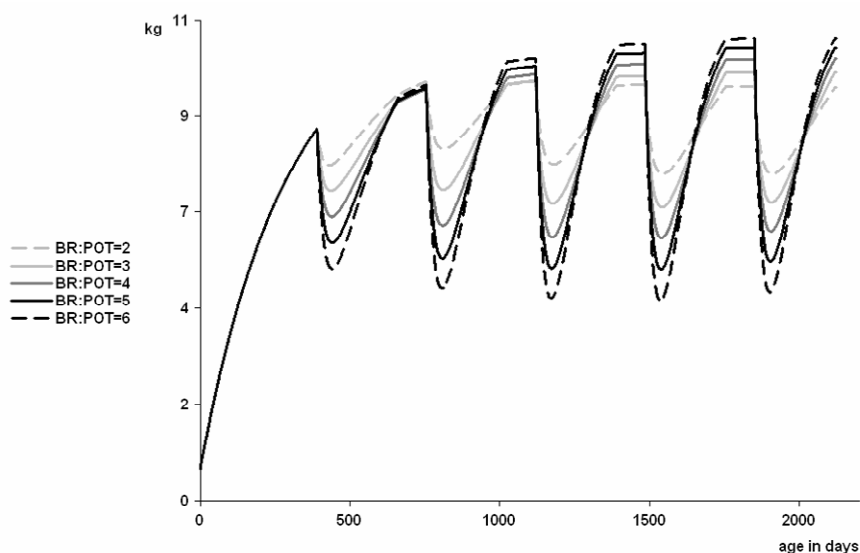


Fig. 3. Simulated kinetics in kg/day of body reserves (BR) of a goat weighing 4 kg at birth, reaching 60 kg at maturity and with a production potential (POT) varying from 2 kg to 6 kg (modified from Puillet *et al.*, 2008).

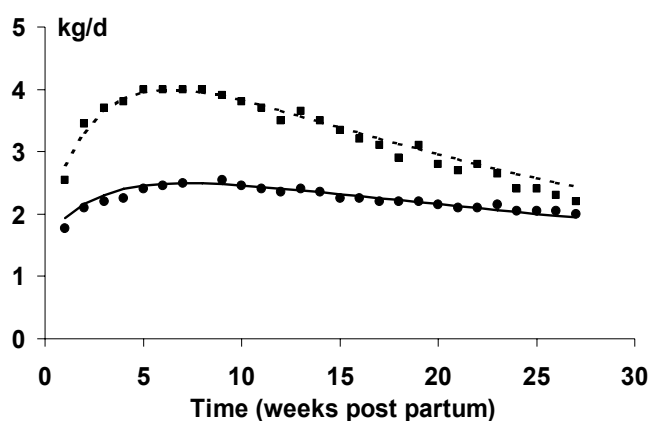


Fig. 4. Comparison between simulated milk yield (---) and dry matter intake (—) and respective data (●■) (average of 72 females from INRA PNA experimental flock).

A. Implications of downscaling

A better understanding of the role of the variability of female's lifetime performance traducing their biological responses to management is crucial to assess whether within herd diversity is an advantage or not for LFS sustainability. Several studies have reported that each animal's varying production responses to a same practice on one hand and the farmers' differing practices depending on the animal status on the other, lead to a diversity of lifetime performances within herds (Lasseur and Landais, 1992; Coulon *et al.*, 1993; Moulin, 2000). This

diversity, in addition to the in-herd distribution of production potential, can have strong consequences on the herd production pattern and on the inter-annual variability of production. On the basis of seven case studies, it has been argued that there is no one-way relationship between lifetime performance diversity, the level of constraint weighing on the system and the type of production project (Tichit *et al.*, 2004b). Tolerating, even seeking, lifetime performance diversity is not a specificity of systems favoring annual herd production stability in uncontrolled environments. It can also be useful in systems which are biologically demanding, for instance Cournut and Dedieu (2002) showed that diversity of lifetime performances in three lambing in two years systems does not mean low level of productivity. However, to date, the question whether the diversity of lifetime performances is an advantage or not for herd long term production has not yet been studied by fully integrating the flexibility that can emerge from female biological response. Cournut and Dedieu (2004) developed a first attempt to incorporate the diversity of lifetime performances into a herd simulator but without any consideration for feeding and with an important data base making it possible to statistically model female responses. In that sense, Puillet *et al.* (2008) modelling approach opens interesting perspectives to explore the emergent properties linked with in-herd diversity. We think that these emergent properties are likely to be different according to changes in feeding system and/or reproductive rhythm. It is crucial to evaluate if they will contribute to reinforce the herd's ability to face a changing environment.

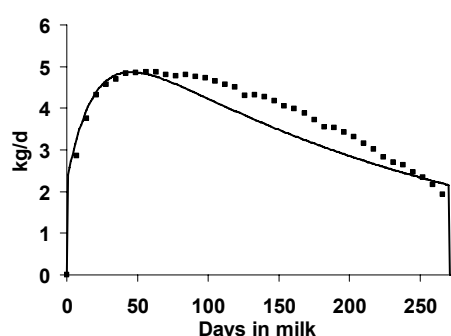


Fig. 5. Comparison between simulated milk yield (—), and data (●■) (average of 92 females from INRA PNA experimental flock).

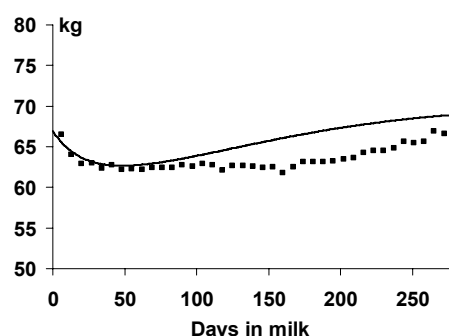


Fig. 6. Comparison between simulated body weight (—), and data (●■) (average of 92 females from INRA PNA experimental flock).

2. Upscaling and the necessity to simplify mechanisms to assess long term impacts of LFS

Over the last 50 years, the loss and degradation of some grassland habitats, through agricultural intensification, have been considered as a primary cause of the severe decline in grassland bird biodiversity (Duncan *et al.*, 1999). Due to their high importance, the remaining original grasslands have benefited from conservation measures since the early 1990's. However, grasslands are not wild but rather anthropic habitats that are economically exploited through grazing. It is now recognised that targeted agricultural practices may contribute to this general goal, eliciting increases in the number or density of species. Many authors have suggested that manipulation of livestock density is a key management tool to conserve birds breeding in grasslands (Norris *et al.*, 1997, Tichit *et al.*, 2005b). Yet the specific grazing regimes that should be used in a long term perspective to favour different species remain largely unknown.

Different approaches have been used to formalize the long term consequences of management. On one side population ecologists have developed population viability analysis (PVA) to assess the effects of habitat quality on species extinction risk (e.g. Beissinger, 1995). Most PVA models do not, however, incorporate explicitly the driver of habitat quality e.g. management as well as do not assess economic and productive consequences of management. Animal production models that have simultaneously assessed production and economic outcomes (Beukes *et al.*, 2002, Tichit *et al.*, 2004a) do not however take management impacts on biodiversity into account. More recently, Tichit *et al.* (2007) have developed a modelling framework, denoted co-viability, which integrates explicitly management dynamics as a driver of habitat quality and habitat quality as a driver of wild species populations. The models, described below, allows to trade-off production and conservation outcomes in a dynamic framework. It combines a minimum of processes representations used in models of grazed grasslands with the long term approach developed by population ecologists. Compared to PUILLET's model, temporal scales are enlarged, but processes at the animal level are not modelled. The co-viability model represents stocking density only which traduces impact on grass sward generated by a group of identical individuals.

The co-viability model represents a grassland ecosystem which is the breeding habitat of two bird species and the feeding resource of suckling cattle (cow and calves). The model comprises two interactive sub-models describing the dynamics of: (i) a grass sward controlled through grazing; and (ii) the bird community. Sward dynamics determine the breeding habitat quality of each bird species as their vital rates explicitly depend on the vegetation structure, i.e. sward height, produced by grazing. This dynamic modelling framework explicitly integrates management dynamics, in terms of stocking density and timing, their impact on habitat quality together with their economic and conservation outputs. The model predicts how livestock grazing, through its impact on habitat quality, may be used to sustain a bird community without penalizing cattle feeding. To perform such a multiple assessment of the grazed grassland, two mathematical frameworks related to the viability of a dynamical system are linked. First, the viability theory is used to reveal viable grazing strategies verifying the compatibility between ecological and production goals at any point in the future. Second, using PVA tools, the extinction risk of the bird community is assessed according to the different levels of habitat quality produced through grazing. To reveal viable strategies, simulations were performed by iterating dynamics of sward biomass and bird populations over a period of 15 years. Four scenarios were tested corresponding to the combination of two levels of habitat quality (homogeneous or mixed) and two grazing strategies (minimal and maximal grazing throughout time).

Model results predict that both minimal and maximal grazing were viable in the sense that cattle feeding requirements were always satisfied while generating suitable sward heights either for homogeneous or mixed habitat quality. In homogeneous habitat quality, both bird species viability could be ensured over the whole time period with both grazing strategies. However in mixed habitat quality, minimal and maximal grazing strategies were associated with contrasted effects on sward height and consequently on bird community persistence. Minimal grazing was characterised by low grazing intensity during late winter and early spring leading to high habitat quality for both species. Maximal grazing corresponded to a higher intensity maintained throughout spring inducing a sequence of high followed by medium habitat quality or the reverse for both species. The solution space of the co-viability analysis is synthesized by Fig. 7 for the four scenarios combining two levels of habitat quality and two grazing strategies. Two of them did not ensure co-viability in the long term as they failed to maintain either population or economic performance above their minimal thresholds. Minimal grazing targeted at mixed habitat quality generated an insufficient economic outcome. Conversely, maximal grazing aimed at mixed habitat quality led to the highest level of production but ensured the maintenance of one species only. Consequently, the combination of maximal grazing and homogeneous habitat quality represented the best compromise in terms of both production and conservation.

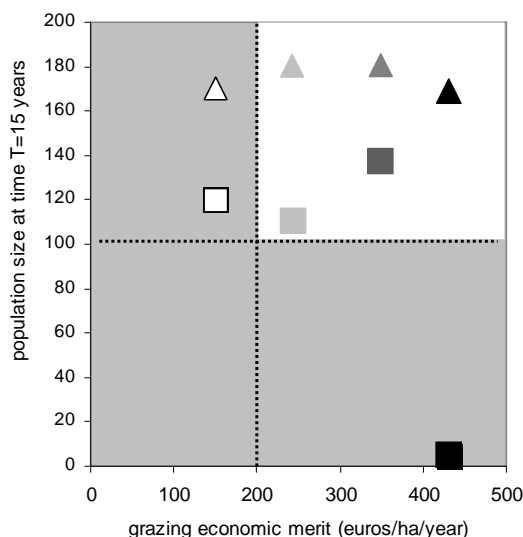


Fig. 7. Solution space (white) for the relation between grazing economic merit and population size at time T=15 years of bird one (square) and bird two (triangle) generated by the co-viability analysis. Colours describe four scenarios combining two level of habitat quality with two grazing strategies: mixed quality – minimal grazing (white) or maximal grazing (black); homogeneous quality – minimal grazing (light grey) or maximal grazing (dark grey). Dotted lines represent production and conservation viability constraints defined in terms of minimal thresholds on population size and economic merit.

Compared with Puillet's model, this model was less formally validated. In its present stage of development the strength of the model lies in the qualitative results showing that production and ecological outcomes involve complex trade-offs that emerge from the interaction between the level of habitat quality targeted and the grazing strategy implemented to manage the grassland system. This modelling framework makes it possible to disentangle the various factors influencing bird biodiversity. It isolates habitat quality as a grazing dependent variable and shows that a fine tuning of this variable is necessary to ensure both production and conservation objectives over the long term. The predicted grazing regime (intensity and timing) were compared to those observed in a large data set in a French grassland area (marais poitevin, $n = 600$ plots). All correspond to existing grazing regimes in the study area and are qualitatively congruent with previous work showing that suitable grazing management for bird species consists in different timing and intensity of grazing (Tichit *et al.*, 2005b). All predicted grazing strategies included spring grazing as observed in the study area. This result is interesting as the exclusion of livestock during spring has been advocated as a desirable option to manage grasslands for the benefit of birds (Hart *et al.*, 2002). The model shows that it is possible to manage suitable level of habitat quality while ensuring livestock feeding.

However, all observed grazing regimes were not predicted by the co-viability model. In particular, model results do not prove the importance of autumn grazing for the more precocious species such as lapwings, as also reported in this area (Tichit *et al.*, 2005a). This situation may be explained by the fact that autumn grazing may play an important role in promoting settlement

the following early spring, but this stage of the bird breeding cycle was not taken into account in this model. Another possible explanation relies in the production constraint considering that cattle demand (used to predict stocking density) never exceeds available biomass. It would be relevant to relax this constraint as in grazed system it is frequently observed that livestock are not always fed to requirements leading to a punctual poorer body condition. This would probably enlarge the range of predicted grazing regimes and would enhance the economic outcome of the different scenarios. Finally, it deserves to stress that this framework remains flexible in terms of complexity and data requirements. We are currently developing a similar model at the scale of a grassland landscape where different habitat conditions are generated by several grazing and mowing regimes.

3. Down and up-scaling open new fields of co-operation with other disciplines

These examples of recent modelling works show that new issues in LFS are likely to call for new integrative modelling developments. These developments open new fields of collaboration between animal production science and other disciplines. The lactating goat model brings a clear illustration on the necessity to reinforce co-operation between researchers working at the LFS level and the animal science community (Gibon *et al.*, 1999). Especially, the incorporation of basic knowledge about individual response to management is likely to help us in increasing our understanding of the biological basis of production processes. This can be essential if we want to achieve a more efficient assessment of LFS sustainability (Blanc *et al.*, 2007). Similarly, the co-viability model shows that environmental impact of livestock can benefit from collaboration with population ecologists. Even if LFS researchers and population ecologists have tackled long term and large spatial scales, the existing approaches in both communities are however unlikely to be integrated straightforward. This integration will require developing specific modelling framework designed at integrating the links between complex processes (natural and management driven) occurring at different time and spatial scales.

V – Conclusion

To conclude we will summarize the main idea of this paper. Modelling is a powerful research tool which can be used to increase our understanding of LFS. First, it is necessary to be extremely clear about the system under study, the modelling objective and the question to be answered using that type of tool. At this stage, an essential tool consists in developing conceptual models in order to formalize thinking and to identify hypothesis, relevant systems components, their interactions and data required for model development. Second, any modeller has to choose to develop a particular type of model. There exist a great variety of models, neither is perfect, all trade-off generality, precision and realism and any modeller should be aware of its model limitations. Third, all models do not involve the same level of constraints in terms of data availability and validation. A complex and detailed mechanistic model will require multiple parameterisations, whereas an empirical model will be easier to calibrate but will not be able to increase understanding in mechanisms. Fourth, the model should be tested in different situations and this will be a crucial stage to fully appreciate and understand its behaviour. For model testing, different complementary strategies can be performed. Internal validation through sensitivity analysis will help to assess if model behaviour is coherent whereas external validation will help to test model outputs against reality. This stage is important in order to assess model domain of empirical validity. Finally, we argue that models are a relevant tool for organising interdisciplinary efforts which are needed to confront new issues faced by LFS.

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